The effects of forest disturbance and fragmentation on fruit-feeding butterflies in Trinidad

Thesis

The effects of forest disturbance and fragmentation on fruit-feeding butterflies in Trinidad

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To Nici, Annie, Toby, mum and dad

with all my love

A pair of *Ithomia pellucida* "blue transparents" coupled in mating

"I found...a perfectly new and most magnificent species of butterfly...the beauty and brilliancy of this insect are indescribable, and none but a naturalist can understand the intense excitement I experienced...on taking it out of my net and opening the glorious wings, my heart began to beat violently, the blood rushed to my head, and I felt...like fainting...so great was the excitement produced by what will appear to most people a very inadequate cause." (Alfred Russel Wallace, 1823-1913).

Contents

Abstract

This thesis explores the use of tropical butterflies as indicators of forest disturbance, fragmentation and forest recovery. The disturbance level of habitats was found to be characterised by the rate of the fraction of species accumulated, with species in undisturbed habitats accumulating more slowly. Undisturbed habitats, but not more disturbed ones, were found to have a vertically stratified butterfly assemblage between the forest understorey and canopy, and certain species were found to be horizontally stratified from the forest edge.

No significant effect of breaks in a forest habitat to the dispersal of certain fruit-feeding butterflies was found, but for species which did not cross breaks, it was not possible to determine whether this was due to low numbers of captures or because breaks acted as barriers to dispersal.

Cissia arnaea (Nymphalidae: Satyrinae) was present in significantly greatest abundance in 30 year selectively logged forest, even though canopy openness was not significantly different from that found in 5 year forest. Conversely, *Colobura dirce* (Nymphalidae: Nymphalinae) was found in greatest abundance in the 0 and 5 year forest and least abundant in the 30 year forest. It is possible that these species could be used to indicate forest recovery following selective logging.

Population size estimates and average residency rates were calculated for *Cissia penelope* and *Morpho peleides* from fruit trap data. Community structure in the *Cissia* genus was explored, and the relationship between local abundance and geographic range size investigated and certain restricted range species were not found to be adversely affected by forest disturbance in Trinidad as expected (Thomas 1991 and Hamer *et al.* 1997).

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Abbreviations

BA	Basal area
BMNH	British Museum of Natural History
B1	Block 1 (area or Block of forest demarcated for logging under the Periodic Block System of forest management in Trinidad)
Dbh	Diameter at breast height (of a tree)
FAO	Food and Agriculture Organisation of the United Nations
FR	Forest Reserve
Gbh	Girth at breast height (of a tree)
GIS	Geographic Information Systems
MRR	Mark-release-recapture
mybp	Million years before present
ORM	Open Range Management of logging in Trinidad
PBS	Periodic Block System of forest management in Trinidad
PSP	Permanent Sampling Plot
WRI	World Resources Institute
ybp	Years before present

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Chapter 1

Introduction

This Chapter introduces the main themes of this thesis. It begins with a description of the different types and extent of cover of tropical forests, followed by estimations of plant and animal species richness found within these forest ecosystems. This is followed by sections on natural and anthropogenic physical disturbance, and the extents and rates of this disturbance. These are background themes to which this thesis was set. This is followed by a review on the reported effects of disturbance on forest ecosystem processes, and the effects on floral and faunal groups. This leads on to answer why forest butterflies were chosen as the indicator group of disturbance in this thesis, and reviews the results of research in this subject area.

1.1. Characterisation of tropical forests

1.1.1. Types and extent of tropical forests

The term 'rain forest' was first coined in 1898 by the German botanist, Schimper, to describe forests which grow wherever the annual rainfall is greater than 2000 mm (80 inches). Although some rain forests are found in temperate regions (broad-leaved evergreen forests in Florida, U.S.A and at the southern tip of South Island in New Zealand), they are found most extensively in the humid equatorial belt between the Tropic of Cancer and the Tropic of Capricorn, 23 degrees and 27 minutes north and south of the Equator. Historically this forest covered some 24,500,000 km^2, but by the late 1980s this had been reduced by 59 percent (Newman 1990). Tropical forest still covers more than six percent of the earth's land, in three major areas, the Americas, Africa and Asia. The largest of these is the American or Neotropical forest, which includes the Caribbean, Central America (including Mexico) and South America, followed by the rapidly disappearing Indo-Malayan Pacific forests with the

least extensive coverage in Africa. The work described in this thesis comes from Trinidad in the Caribbean, part of the Neotropics.

Tropical seasonal forests are less extensive than true rain forests, but since they have many features in common, collectively they are known as 'moist forests'. These moist forests are known as dryland moist forests to distinguish them from mangrove and swamp forests (palm swamp and marsh forests) which are wetland moist forests. Dryland moist forest types can been divided into three forest categories with reference to altitude, as shown in Table 1.1 below. Information from 'The Conservation Atlas of Tropical Forests for the Americas region' (Harcourt and Sayer 1996).

Table 1.1. Dryland moist forest types as categorised by Harcourt (1996). FAO (1993) give no detailed descriptions of the different forest formations or zones in which they occur.

Lowland moist forest	**Submontane forest**	**Montane forest**
tropical evergreen rain forest	lower montane moist forest	montane wet forest
tropical semi-evergreen rain forest	lower montane wet forest	montane rain forest
tropical semi-deciduous forest	lower montane rain forest	cloud forest
tropical humid forest		
tropical perhumid forest		
riverine/gallery forest		
evergreen seasonal forest		
semi-evergreen seasonal forest		

The third forest category covered in Harcourt (1996), along with wetland and dryland moist forests, is the dryland dry forests which include dry forests (dry deciduous forest, xerophytic forest, tropical dry forest, dry evergreen forest and dry semi-evergreen forest) and pine forests.

In terms of all forests with a canopy cover greater than 10 %, over half of the world's tropical forest, 9,073,890 km^2, are found in the Neotropical region, with the vast majority of this (91.2 % or 8,279,460 km^2) in South America, with 67 % of that in

Brazil. Only 44,250 km^2 or 0.5 % is in the Caribbean and 750,180 km^2 or 8.3 % is in Central America (FAO 1997). In its 1993 report, FAO determined that the tropical forest of South America (excluding Surinam, Guyana and French Guiana which were considered part of the Caribbean in this report) was dominated by the two ecofloristic zones (FAO (1993) give no detailed descriptions of the different forest formations or of the zones in which they occur) of tropical rain forest (49.5 %) and moist deciduous forest (32.1 %), followed by hill and montane forest (13 %) (FAO 1993). The Caribbean's forest cover was mainly tropical rain forest (75.8 %), then moist deciduous (18 %) and to a lesser extent hill and montane forest (6.1 %). In contrast to this, Central America was principally hill and montane forest (56.2 %), followed by moist deciduous (20 %) and tropical rain forest (18.3 %). These forest areas, and the areas of forest coverage for the three other ecofloristic zones categorised by FAO (1993), are shown below in Table 1.2.

Table 1.2. Area of forest formations (km^2) for Central America, Caribbean (including Suriname, Guyana and French Guiana in FAO 1993 but included in Tropical South America in FAO 1997), Trinidad - values shown separately in addition to being part of the Caribbean, and Tropical South America (from FAO 1993). Total forest 1990 (FAO 1997) values are different from those reported for 1990 in FAO 1993, due to new assessments of forest cover and updated forest inventory information.

Forest formation	CENTRAL AMERICA	CARIBBEAN	Trinidad	TROPICAL S.AMERICA
Total forest 1990 (FAO 1997)	798,120	48,160	1,740	8,512,230
Total forest 1995 (FAO 1997)	750,180	44,250	1,610	8,279,460
Total forest 1990 (FAO 1993)	680,970	471,150	1,550	9,181,160
Tropical rain forest	124,400	357,070	1,550	4,543,090
Moist deciduous forest	135,880	84,830	0	2,943,060
Dry deciduous forest	15,900	490	0	449,440
Very dry forest	7,590	50	0	10,450
Desert	14,240	40	0	16,160
Hill and montane forest	382,940	28,670	0	1,218,950

1.1.2. Plant and animal species richness

Whereas a relatively rich temperate forest may have less than ten different species of tree per hectare, between 155 and 283 species of tree over 10 cm in diameter at breast height (Dbh) have been recorded in a hectare of tropical rain forest in Peru, upper Amazonia (Gentry 1988). Within a 0.5 m^2 quadrat placed on the ground in Peruvian lowland tropical forest, the leaves of 50 different species of tree were found (Newman 1990). Another example illustrating the tree species richness of tropical regions, is that the state of Brunei in Borneo, South-East Asia, boasts 2000 tree species compared with the entire country of the Netherlands, seven times larger in area, which has 30 (Newman 1990).

The vertebrate fauna (amphibians, reptiles, fish, birds and mammals) of the tropical region, like the flora, is species rich. Over 1000 species of amphibian and 1100 reptile species have been recorded in South America (Harcourt and Sayer 1996). Approximately 500 reptile species are known from the Neotropical lowland rain forest area, some 300 of which are endemic to this region (Dixon 1979), but Mexico is the individual Neotropical country with the highest species count of 717 species (Harcourt and Sayer 1996).

The richest freshwater fish fauna in the world is found in the Neotropics with more than 2400 species having been described. The richest river basin in the world in terms of freshwater fish is the Amazon basin, with over 1300 species (Lowe-McConnell 1987). The richness of this fauna is highlighted by the fact that over 100 species of fish have been found in a 6 x 30 m rocky pool from the upper Rio Negro, Brazil (Goulding *et al.* 1988).

Of the 3300 Neotropical avian species, 1300 are forest species. This compares with 800 forest bird species in Southeast Asia and 400 in Africa (Karr 1989). Latin American forests are extremely rich in raptors and woodpeckers (Picidae) and a

diverse radiation of parrots (Psittacidae) and trogons (Trogonidae) (Karr 1989). Avian species richness is highest in Colombia, compared with anywhere else in the Neotropics, with 1721 species, and the highest forest count is for Manu National Park in Peru, where Terborgh and colleagues have identified over 550 species of bird (Robinson and Terborgh 1990).

Typical lowland rain forests in the Neotropics can contain over 120 mammal species, with Mexico, Central America and South America having 1116 recorded mammal species (Harcourt and Sayer 1996).

At the Royal Entomological Society's Symposium on Insect Diversity in 1977, Southwood presented a pie-chart representing the relative contributions of the then 1.4 million described species of animals and plants and pointed out the striking dominance of insects (57 % of the described species), the beetles representing 25 % of all described species (Stork 1988). In 1988 the figure of described species stood at 1.82 million with the relative proportions remaining similar. How does this value of one million plus described insect species relate to the real number of species of insects and other arthropods ? Estimates have varied from 3-5 million (May 1986), 10-80 million (Stork 1988) to 30 million for tropical arthropod species (Erwin 1982). May (1986) put forward the proposition that, to a good approximation, all organisms are insects, because they so overwhelm other taxa in species number. Whatever the actual total number of insect and arthropod species, it is evident that invertebrates, particularly in tropical rainforests, are a major source of the world's total biodiversity.

It has been estimated, that perhaps as many as 75 to 90 % of all insect species are confined to tropical moist forests (Sutton and Collins 1991). It is also clear that the vast majority, 67 - 99 % (using the most conservative and most extreme of recent estimates), are undescribed. How many will have been lost before they have been described ? As Stork (1988) points out, "if it has taken 230 years since Linnaeus to describe one million species of insects what chance do we have of describing the other

nine (or 79!) million ?", especially with present-day deforestation rates. Compared with temperate regions such as the U.K. which has 58 species of butterfly, the tropical regions are much more species-rich with 630 species known from Trinidad, 2316 from Venezuela in South America and 7179 species known from the Neotropical region as a whole (Beccaloni and Gaston 1995).

The biodiversity of forest habitats can be measured in terms of floral and faunal species' richness, abundance and diversity. Bioindicators or 'predictor sets' are now the focus of much research (Burbidge *et al.* 1992, Cranston 1990, Dunlop *et al.* 1985, Jones 1984, Kitching 1993, Kremen 1992, Landress *et al.* 1988, Majer 1983, Yen 1987) because it is obvious that resource limitation will never permit the inventory or monitoring of all groups. It is therefore generally necessary to select one or more groups on the basis of their ability to tell us something about the total biodiversity of that system.

Some of the precautions that need to be addressed when using indicator groups are the heterogeneity of feeding habits and the responses to environmental change (see sections below) that some large taxa may exhibit. Although some insect orders such as the Odonata (dragonflies and damselflies) are all predators and represent a single feeding habit, most orders contain species from a range of trophic levels and feeding habits. The range of feeding habits tends to narrow with passage down the taxonomic hierarchy, for example, from order to family to genus. A good example is the order Coleoptera which although ecologically diverse, includes the families Coccinellidae which are almost all predators and the closely related family Phalacridae which are primarily mycophagous.

There is little available evidence, however, indicating that the diversity of one group represents the diversity of other components of the community. Many biodiversity surveys assume that samples of some subset of species, most often flowering plants and selected vertebrates, adequately represent all others, including lower plants and

invertebrates. This is the "umbrella" hypothesis. There is little evidence to support this. In Majer's study cited above, for example, variation in ant species richness was explained by several factors, plant species richness accounting for only 24 % of the variation in the number of ant species. A study in South East Australia (Yen 1987) of plant, vertebrate and beetle communities at 32 sites found no significant correlation between the number of species of vertebrates and the number of species of beetles sampled from the same habitats. No correlation was found either between vertebrate and ant species richness at sites in South West Australia (Burbidge *et al.* 1992).

Exceptions to this come from studies in Australia and New Zealand. The species richness of ants in Australia has been found to reflect the species richness of Collembola, termites and grasshoppers, and also the abundance of a range of animals from various arthropod orders in a variety of forest and rehabilitated mines (Majer 1983). A positive relationship has also been found between the percentage of native New Zealand beetle species and the percentage of native vegetation in the habitat under study (Crisp *et al.* 1998)

Historically, flowering plants and vertebrates have been used as indicators, although they represent only a small fraction of the total biodiversity. There is an increasing emphasis on the use of invertebrates in biodiversity surveys because of their diversity, abundance and major functional significance. The fact that many large vertebrate species tend to range across many habitats, also limits their value as indicators of specific habitats (Landress *et al.* 1988).

The greater the species richness of a species group, the more sensitive it is likely to be to habitat change and thus the more useful as an indicator of changes in ecosystem processes. This suggests that studies of taxa exhibiting extreme diversity, notably the insects, are likely to demonstrate most conclusively whether or not the ecosystem regains a form equivalent to that occurring before the disturbance (Johns 1992b).

1.1.3. Nàtural forest disturbance

White and Pickett (1985) define a disturbance as a relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment. Such disruptions may vary in distribution, frequency, predictability and severity. They also may be synergistic with other disturbances, such as long periods of drought, or may increase the risk of a fire outbreak (White and Pickett 1985).

Reviews of tropical forest dynamics emphasise the importance of canopy openings in the structural and compositional dynamics of many tropical forests (Brokaw 1985, Denslow 1987, Martinez-Ramos *et al.* 1989). Forest disturbance is caused by tree falls which open the forest canopy, creating light gaps. 'Gap-phase regeneration' describes the events following a tree fall until it has finally been replaced by a new canopy tree (Hubbell and Foster 1986). It is felt that the creation of gaps is the principal or only means by which most tree species remain represented in closed-canopy forests (Hubbell and Foster 1986).

Natural gap formation in Neotropical forests, as described by Hartshorn (1990) is 'caused by any number of natural occurrences such as bole, branch, or crown breakage, fall of liana tangles, "windthrow" (root tip-up), the domino-effect of a large tree taking down others, localised winds, tropical cyclones (hurricanes), lightning, landslides, and simply the death of a standing tree'.

The direct result of a treefall is a gap in the forest and an area of affected vegetation. The process of a tree falling, the fallen tree itself, together with the resultant hole in the canopy and accumulated debris on the forest floor is known as gap formation (Halle *et al.* 1978). The initial size of the gap is decisive in the course of subsequent regeneration processes. A large gap may take longer to recover because succession

starts at the pioneer phase, while a smaller gap may be closed rapidly by the crowns of trees surviving or recovering from the impact of the treefall.

Gaps in the forest canopy are important for the regeneration of many rainforest species and represent a different micro-environment compared to the forest understorey. Not only is light quantity enhanced in gaps (Chazdon and Fetcher 1984), but there are also differences in light quality, soil and air temperature, nutrient and water availability in the soil, and water saturation deficit in the air (Denslow 1987, Schulz 1960). The dynamics of tropical forest gap formation, recolonisation and the process of succession which leads to the eventual closure of the canopy by primary tree species, have been well documented (Brokaw 1982, Halle *et al.* 1978, Hartshorn 1978, Hubbell and Foster 1986, Hubbell and Foster 1987, Sanford *et al.* 1986).

Data collated from four Neotropical forests (Hartshorn 1990) suggests an average annual level of gap formation of about 1 % per year and about 100m^2 per gap.

1.1.4. Anthropogenic forest disturbance

The heightened threat to tropical forest ecosystems from human population increases is exacerbated by the imbalance in world population distribution. Approximately 4100 million people, or just over 77 % of the estimated world population, lived in the less developed countries, or the Third World, in 1990 (Data from United Nations Population Division, quoted in World Resources Institute, 1992). Projected estimates for the year 2025 indicate that this figure will have risen to 84 % of the world's population living in Africa, Latin America, Asia and Oceania (excluding Australia and New Zealand) (World Resources Institute, 1992). Such growth in the population of the developing world makes the continuing deforestation of tropical lands an inevitability (Sayer and Anadu 1989). Squatting, shifting cultivation, hunting, enhanced levels of timber extraction and forest fires (spread more easily as forests become more disturbed), are some of the most widely seen effects of this increased

pressure, which differ in their relative importance from region to region. The main factors implicated in the deterioration of Zaire's tropical forests in Africa, for example, were shifting agriculture, fuelwood consumption and fires in open forests and savannas (Khasa *et al.* 1995).

Original 1981 FAO estimates (Whitmore and Sayer 1992) of global tropical closed plus open forest clearance of 11.3 million hectares per year for 1981-5, were estimated to have increased to 15.4 million hectares per year between 1981-1990 (FAO 1993). After a re-evaluation of the deforestation rates that had been used for some Asian countries, a higher estimate of 17 million hectares per year for the period 1981-1990 has been put forward (Whitmore and Sayer 1992). More recent estimates over the period 1990-1995, are 13.7 million hectares per year (FAO 1997), suggesting that although still high, the rate of loss of natural forests in developing countries has slowed since the last decade.

Comparisons of estimates of forest loss are made difficult by inconsistent use of definitions of forest cover types and deforestation (Whitmore and Sayer 1992). Whereas forest and non-forest, such as grasslands, are relatively easy to distinguish on remote-sensing images, it is more difficult to monitor the various kinds of disturbance because it is very difficult to discriminate between old-growth forest and regenerating secondary forest. Workers at the University of Hertfordshire and the Open University, are presently working on satellite radar images of Guyanese rainforest and from ground truthing in the field, attempting to refine the resolution to which features such as roads and gaps can be interpreted (Gillman and Teeuw 1995), and relating this to butterfly diversity. Currently the smallest gaps that can be detected are ca. 50 x 50 m, although this depends on ground conditions (e.g. it is easier to detect gaps with water in them than without). In this study, forest disturbance levels were characterised from knowledge of their prior history and using vegetation structure and canopy openness measurements.

A reduction of habitat quality (see sec. 1.2.1) also results from increased anthropogenic activity. It has been estimated that 92.1 million ha of closed forest were lost between 1980 and 1990 (FAO 1997). Of this, 40 % (36.6 million ha) went to 'other land cover' which includes permanent agriculture, cattle ranching and water reservoirs, representing a complete loss of cover and woody biomass; 26 % (24.1 million ha) went into shrubs and short fallow agriculture which represents deforestation, but with some woody biomass remaining; 20 % (18.2 million ha) went into open forest or long fallow shifting cultivation, representing degradation involving the loss of approximately half its biomass; 10 % (9.2 million ha) went to fragmented forest, representing partial deforestation, with a loss of approximately two-thirds of the original forest cover and 4 % (4 million ha) went to agricultural or forestry plantations. The preservation of intact swathes of rain forest, although highly desirable, is unlikely, and so the value of conserving these degraded habitats alongside pristine forest, must be investigated.

The reduction of area covered by tropical forest and habitat quality, as described above, is not the only deleterious consequence of increased anthropogenic pressures on tropical forests. Blocks of contiguous forest will also become fragmented into pockets of smaller sized areas of forest, reducing the area of core forest and increasing the edge to core forest ratio. From spatial analysis of forest fragmentation based on high-resolution remote sensing in southwestern Ivory-Coast, forest fragments were mainly found close to the deforestation front (Chatelain *et al.* 1996).

1.2. Effects of disturbance on the tropical forest ecosystem and its flora and fauna

The rapid fragmentation and reduction in area and quality of tropical forest, combined with the concentration of the world's species in tropical forests, led Myers in 1983 to the view that a significant proportion of all species of plants and animals would become extinct in the following few decades and perhaps as many as 25-30 percent by AD2000 (Myers 1983). Evidence of this mass species loss has not yet been observed. However, it has been suggested that "the regions where tropical moist forests are expected to be destroyed in the next 30 years contain an estimated half of the world's plants. If half of these species will be at risk when the forests have been reduced to less than 10 % of their original extent, I estimate the extinction of perhaps 65 000 species, a quarter of the world's total, within the next several decades" (Raven 1990). The Joint IUCN-WWF Plants Programme (Heywood and Stuart 1992) arrived at similar estimates of up to 60,000 plant species becoming extinct or suffering from severe genetic erosion by the middle of the next century, if present trends of habitat loss were to continue.

A few authors (Lugo 1988, Simon 1986) have argued to the contrary that there is little evidence to support such mass species extinction estimates, and that the risks inherent in tropical forest deforestation have been exaggerated.

1.2.1. Ecosystem effects

Disturbance may alter aspects of the forest's abiotic environment, including changes in temperature, humidity, light and rainfall levels that penetrate the canopy to the forest floor. Gap size, shape, aspect, and the height of the surrounding vegetation as well as treefall debris in the gap itself, all influence gap light, temperature, moisture, and wind regimes (Brokaw 1985, Denslow 1980). "Light in gaps is higher in intensity, lasts longer during the day, and is of a different spectral quality than in the understory of

the closed-canopy forest. Soil and the air layer near the ground are often much hotter in gaps during the day, and cooler at night" (Hubbell and Foster 1986). Humidity is often lower in gaps than in surrounding forest, but soil water content may actually be higher because of reduced root uptake and lower transpirational water loss from gaps (Lee 1978). Soil nutrients in gaps are enriched in local patches, particularly in areas adjacent to the decaying fallen tree and in the disturbed soil of the uprooted tree (Hubbell and Foster 1986).

When surface soil properties were compared among disturbance classes associated with a single species selection harvest study, initiated in 1979 in the Brazilian Amazon (McNabb *et al.* 1997), it was found that concentrations of all elements showed residual effects 16 years after harvests with N, P, K and C being inversely related to disturbance intensity while Ca and Mg levels, as well as pH were directly related.

Clearance of large areas of tropical forest has been found to cause significant losses of soil carbon and nitrogen which tend to decline further under continuous cultivation (Ross 1993). The reasons for this reduced fertility include accelerated soil erosion, loss of litter influx after canopy removal and enhanced decomposition and nutrient mineralisation rates after forest clearance (Ross 1993).

1.2.2. Plant species

Forest disturbance affects the floral composition of the forest directly and indirectly. Logging practices, for example, alter the tree species assemblage in a selective manner by extracting individuals of a limited range of marketable tree species. This range can be narrow, as in Guyana where the logging industry has been almost exclusively based on the extraction of greenheart *Chlorocardium rodiei*, where this species accounts for over 45 % of fellings and 70 % of exports, even though it comprises only 1.5 % of the exploitable timber (NFAP 1989). In Peninsular Malaysia, there are around 2,500 tree species, of which 700 reach a size large enough to be usable (basal

girth >1.35 m). Of these species, 402 are considered commercial, but even at he peak of timber exportation, less than half (30 species and species groups) were exported in significant quantities (Johns 1992a).

In Malaysian dipterocarp forests dominated by consociations of *Dryobalanops aromatica* and *Shorea curtsii*, the number of trees felled may reach 72 / ha, but more usually 14 / ha (Whitmore 1984). On the other hand most Amazonian *terra firme* forests yield only 3-5 trees / ha (Johns 1992a) and some African forests as few as 1.1 / ha (Bullock 1980). Although this process should selectively remove species from the assemblage, the mortality caused to other trees in the logging process far outweighs the mortality of tree extraction (Johns 1992a). The result is that damage is spread over all tree taxa, with the damage being essentially random (Johns 1988). In this scenario of effectively random destruction, all rare species will be susceptible to depletion but in particular those which are also valued timber species. A species such as Brazilwood, *Caesalpinia echinata*, has already been eradicated from most of its former range in the Amazon basin for this very reason (Johns 1992a).

Tree species richness per unit area may be reduced as a result of logging, especially when only small areas are considered, and this loss may be influenced by the level of basal area reduction. Through the forest as a whole, however, there may not be a reduction in species richness or diversity. In fact, results from Queensland have suggested that logging reverses a natural loss of diversity that occurs as a forest matures after disturbance and its pioneer species die out (Nicholson *et al.* 1988). Following logging, the diversity of tree species in a forest may increase as a result of the rapid germination of pioneer tree species. In the Neotropics these may include species representing the Euphorbiaceae genera *Cecropia* and *Vismia*, and legumes such as *Inga* species.

The effect of depleting tree species in a forest are exacerbated further if that species is also of high wildlife value. It has been estimated that as few as one percent of the trees

in a slightly seasonal rain forrest in Peruvian Amazonia may support the bulk of the frugivorous animal populations for several months of the year (Terborgh 1983). Food resources for frugivores tend to be widely dispersed in the forest, those for folivores often less so. The distribution of trees becomes more patchy following intensive logging (Johns 1988), which may necessitate changes in ranging and foraging behaviour among animals. Species unable to adapt would be placed at a competitive disadvantage. It has been suggested that the initial loss of food sources during logging may be buffered by greater levels of fruiting and new leaf production stimulated by the opening of the canopy (Chivers 1972). Eleven years after logging in forest in Brazil, it was found that although new leaf production was similar with unlogged forest, fruit production was significantly reduced (Johns 1986).

Singapore has lost 99.8 % of its primary forest but only 29 % of its native vascular plant species (Turner *et al.* 1994). Epiphytic species seem extremely prone to extinction with 62 % of species being lost, including all of the mangrove epiphyte flora (Turner *et al.* 1994). A four hectare forest fragment in Singapore, isolated for a century, was found to have lost 50.9 % of plant species (Turner *et al.* 1996). These losses were not distributed evenly across plant life-form groups. Tree species were less likely to go extinct than shrubs, climbers or epiphytes. Individual longevity may be the major correlate with persistance of plant species in isolated forest fragments.

Work carried out in Trinidad (Clubbe and Jhilmit 1992) on the Open Range Method (ORM) of tree harvesting (unlimited extraction) compared with primary forest and the Periodic Block System (PBS) of selective logging (See Ch.2 for further details on these two management practices), revealed the deleterious effects of ORM on the ground level epiphyte flora (Clubbe, *pers. comm.*). Between 7 and 9 % community similarity was found (Motyka's index of community similarity) between the the epiphyte fauna of the ORM and two PBS habitats and a primary forest habitat. In contrast, Motyka index values of 73 % were found between primary forest and forest logged six years previously and 83 % with forest logged 23 years before (Clubbe,

pers. comm.). The number of epiphytes on remnant trees in Mexico, left after conversion from forest to pasture, was found to be negatively correlated with the distance from the forest border (Hietzseifert *et al.* 1996). Epiphyte numbers on these remnant trees were found to be within the range found in the two forest plots, although there was a significant difference between these forest plots, possibly due to differences in humidity levels.

Extreme levels of disturbance, as found when forest clearance is undertaken, has dramatic consequences for the tree species compositon of the forest. Rainforest in Puerto Rico, which had previously been cleared for timber production, was found to be dominated by successional tree species 50 years after secondary succession (Zou *et al.* 1995), although it did not differ in tree basal area from adjacent mature forest.

1.2.3. Vertebrates

Vertebrates have been well studied historically, because of their close association with humankind (food, hunting, farming, pets). The appeal of many vertebrate taxa to the wider public and amateur naturalists has lead to a lot of research on such groups as the birds for example. The results of research on the effects of logging on various vertebrate groups is detailed below and summarised in Table 1.3.

Few consistent long-term changes in primate densities were recorded 12 years after logging in Peninsular Malaysia (Johns 1989), although examination of female-infant ratios revealed that some species may be better able to survive than others (*Macaca fascicularis*, *Hylobates lar* and *Presbytis obscura* as opposed to *P. melalophos*). Similar results of little evidence of changes in primate density were found in a long-term Ugandan study (Howard 1986).

Increased levels of disturbance one year after selective logging in French Guiana, resulted in an overall 27-33% decrease in avifaunal species richness (Thiollay 1991).

A reduction in both the number of understorey bird species and their abundance was also found by workers looking at the edge effects of forest fragmentation in Brazil (Lovejoy *et al.* 1986) and in peninsular Malaysia (Johns 1986). A third of the rain forest bird species were found to disappear after selective logging in Liberia, West Africa (Kofron and Chapman 1995), whereas deforestation resulted in a 70 % loss of species (Kofron and Chapman 1995).

Thiollay (1995), investigating bird community composition in traditional agroforests and primary forests in Sumatra, found that species richness, diversity and equitability were all significantly lower (12-62 %) in every agroforest than in primary forest (Thiollay 1995). Coefficients of similarity between the natural and managed communities were also all found to be relatively low (0.43-0.55). Of those species recorded in sampling, 56 % were seen to decrease significantly or disappear from agroforests, whereas only 22 % appeared or increased. The species most affected by the conversion of primary forests were large frugivores and large insectivores of the canopy and low understorey, or terrestrial interior forest specialists (Thiollay 1995).

Table 1.3. A summary of the reported responses of vertebrate taxonomic groups to forest disturbance

Taxonomic Group	Disturbance	Results	Study country	Reference
Birds	Selective logging	Decrease in species richness (27-33%) one year later	French Guiana	Thiollay, 1991
Understorey birds	Forest fragmentation	Decrease in species richness and abundance	Brazil	Lovejoy *et al.*, 1986
Birds	Selective logging	30% decrease in species richness	Liberia	Kofron, 1995
Birds	Deforestation	70% decrease in species richness	Liberia	Kofron, 1995
Birds	Agroforestry compared with primary	12-62% decrease in species richness; 56% of species decreased significantly or disappeared; 22% appeared or increased	Sumatra	Thiollay, 1995
Birds	Shifting cultivation	young secondary growth (<10 yrs.) less similar to other habitats; 13-17 yr. secondary growth and forest understorey,most similar avifaunas	Colombia, South America	Andrade, 1994
Birds	Logging	After 10 yrs. 188 of 193 species found in unlogged forest returned	Peninsular Malaysia	Johns, 1989
Primates	Logging	No change in density 12 years later	Malaysia	Johns, 1986
Primates	Logging	No change in density	Uganda	Howard, 1986
Small mammals	Forest fragmentation by flooding	Rapid decrease in species diversity in small islands, dominated by a few species	French Guiana	Granjon, 1996
Large mammals	Forest fragmentation by flooding	Increase in density as islands diminish in size	French Guiana	Granjon, 1996
Bats	Not reported	2 species, 75% of individuals in disturbed forest; 3 most dominant species made 53% of individuals in undisturbed forest	Central America	Pine&Wilson unpublished *In* Johns 1992
Mousedeer	Selective logging	Densities negatively correlated with the proportion of disturbed forest	Northern Borneo	Heydon, 1997

Shifting cultivation practices are often reported to have negative effects on the forest fauna, but this is not always the case. Looking at the avifauna of regenerating one-hectare crop fields in the Colombian Amazon (Andrade and Rubiotorgler 1994), for example, workers found little difference between species richness and number of individuals found in the different habitats, although young secondary growth, less than ten years, was less similar to other sites, whereas older secondary growth between 13 and 17 years of abandonment and forest understories, had the most similar avifauna. Andrade and Rubiotorgler concluded that abandoned crop fields older than ten years mimicked the natural patch dynamics of the forest, making this shifting cultivation practice an example of a potentially sustainable use of tropical forest (Andrade and Rubiotorgler 1994).

It has been contended that perhaps avian communities which have evolved in areas of unstable ecoclimatic histories may be more robust to change than those which evolved in places of paleoecological stability, although the studies from which these contensions were summised do not lend themselves to rigorous testing.(Danielsen 1997).

The response of a faunal group to the changed conditions of logged forest can often be unexpected. For example, hummingbird communities in neotropical rainforest are generally coadapted with communities of flowering plants, with different hummingbird species diverging in bill shape to exploit flower species of particular corolla design. In regenerating logged forest, much of the available nectar is present in colonizing shrubs and climbers of generalised corolla shape (Feinsinger 1976), with the result that social organisation of the hummingbird community changes to one of aggressive defence of resources (interference competition). Hummingbirds found in logged forest tend, therefore, to be transient species, species richness tending to drop in small isolated fragments (Willis 1979), which might not be expected from examinations of ecological attributes of the species concerned.

In a study on the effects of forest fragmentation caused by flooding, workers in French Guiana found that for small mammals, a strong and rapid decrease in species diversity on small islands, with a few species dominating the communities (e.g. *Proechimys* sp. for the terrestrial small mammals and *Artibeus obscurus* for the bats) (Granjon *et al.* 1996). Large mammals increased in density throughout the study period as the area of available land diminished (Granjon *et al.* 1996). Other studies on vertebrates, and invertebrates (see Section on invertebrates below) have also discovered this dominance by a few species in logged forests. For example, in a central American bat fauna, two species of one genus made up 75 % of a total netted sample in disturbed forest, compared with the three most dominant species making up 53 % of individuals in the unlogged forest (Pine & Wilson, unpublished data *In* Johns, 1992). Similarly in southern India, a few species of birds dominated a number of disturbed forest avifaunas (Beehler *et al.* 1987).

In northern Borneo, mousedeer densities have been shown to be negatively correlated with the proportion of severely disturbed forest, and positively correlated with the availability of potential food resources (Heydon and Bulloh 1997). Heydon and Bulloh found that mousedeer appeared to be more adversey affected by selective logging than other frugivorous ungulates or primates within the same forest, a possible reflection of the limitations in their dietary flexibility imposed by the effects of a small body mass on energetic requirements and digestive capabilities.

When the impact of slash and burn shifting cultivation, known as 'jhum' cultivation, in Northeast India on diurnal squirrels and primates was investigated, an emphasis on the need to maintain mature forest and late-successional (greater than or equal to 25 years) vegetation, in order to conserve several of these species was made (Raman 1996).

Few long-term studies of the effects of forest disturbance have been undertaken. One long-term study looking at the avifauna of logged and unlogged forest in a Peninsular

Malaysian site, found that ten years after the logging event, all but five of the 193 species found in unlogged forest had returned (Johns 1989).

1.2.4. Invertebrates

Studying the effects of disturbance and fragmentation on floral and faunal taxonomic groups must be undertaken if we are to implement forest management strategies which will ensure the maintenance of the world's biodiversity. "Consequences for species survival of the degradation, partial clearance and fragmentation of large forest areas are simply not known though biologists have begun to think about the problem" (Whitmore and Sayer 1992). "There is regrettably little information available concerning the responses of many species groups, however (to forest disturbance). Current views are biased by the responses to larger animals, which are only a part of the total biological diversity of the forests. While admitting the limitations of current knowledge, the continuing loss of undisturbed forest can only mean that managed areas will be a principal hope for forest species of all types" (Johns 1992a). A global research priority, therefore, must be the continued assessment of the effects of forest disturbance on the forest and its wildlife, and a determination of the value of these degraded forests to conservation. Johns, 1992,has also stated that "the greater the species-richness of a species group, the more sensitive it is likely to be to habitat change and thus the more useful as an indicator of changes in ecosystem processes. Studies of invertebrates are likely to demonstrate most conclusively whether or not managed forests are regaining a community equivalent to that of unlogged forest". Invertebrate groups have often been proposed as potential indicators of habitat disturbance because of their close link with the vegetation of that habitat, in terms of adult and larval hostplant specificities, although few studies have proved this empirically (see section 1.1.2 for more detail on the use of indicator groups).

Termite species richness in southern Cameroon was found to be greatest in old secondary and plantation forest, followed closely by near primary forest, the least

disturbed habitat (jack-knife estimates showed no significant differences between these three plots), and lowest in two severely disturbed plots (Eggleton *et al.* 1995). This enhancement in species richness at intermediate levels of disturbance (Connell 1978) is in contrast to the pattern observed with termite species in Sarawak (Collins 1980) and other invertebrate groups such as moth species in Malaysia (Holloway *et al.* 1992) and scarab beetles in Manaus, Brazil (Klein 1989), where a decrease in species richness and species diversity was found as forest habitats became more disturbed and fragmented. Mosquito species have been used as indicators of forest degradation (Dorville 1996), and tiger beetles (Coleoptera: Cicindelidae), proposed as world-wide bioindicator species (Pearson and Cassola 1992), have been found to be appropriate indicators of forest degradation in Venezuela (Rodriguez *et al.* 1998). Forest-floor species assemblages were found to change significantly with the degree of forest disturbance and each stage of disturbance was characterised by a particular subset of species (Rodriguez *et al.* 1998).

Four habitats in Costa Rica, increasing in level of disturbance along a gradient from primary forest, abandoned cacao, productive cacao to productive banana plantation, were investigated in terms of the ground-foraging ant community (Roth *et al.* 1994). The diversity of the ground-foraging ant community was significantly reduced with increased disturbance. Ant diversity was not different for forest and abandoned cacao except in terms of evenness, with the forest having a more even distribution of species (Roth *et al.* 1994).

Johns (1992b) has postulated that the greater the species richness of a species group, the more sensitive it is likely to be to habitat change and thus the more useful as an indicator of changes in ecosystem processes. Studies of invertebrates are likely to demonstrate most conclusively whether or not managed forests are regaining a community equivalent to that of unlogged forest (Johns 1992a). Data in general which relates the effects of selective logging upon insect faunas are lacking (Sutton and Collins 1991).

One of the largest Orders of insects and also most popular insect groups are undoubtedly the Lepidoptera. Whilst much of this interest lies in the realms of philately, much amateur and professional time has been spent on the study of these insects.

"The network of protected areas in tropical forest has largely been set up on the basis of protecting vertebrates, with very little consideration of insect distributions, mainly because these are so inadequately known. Although detailed evidence is lacking, it is unlikely that insects follow the patterns of vertebrate distribution. A policy of protecting arthropods under the umbrella of vertebrate sites is therefore unsound. Plants are better indicators of insect-rich habitats. Nevertheless insects and their allies are so much more diverse and specialised that endemism is far ore widespread and localised. The protected areas network needs to reflect these properties as much as possible" (Sutton and Collins 1991).

"First and foremost among the target taxa are the butterflies" (Sutton and Collins 1991). "Successful conservation of insects turns on adoption of simple techniques of sampling and analysis, together with the selection of a small number of indicator groups, of which butterflies and dragonflies are prime candidates" (Sutton and Collins 1991). Therefore, to study the effects of tropical forest degradation, we chose the Lepidoptera, in particular the fruit-feeding butterflies, as our indicator group, to explore the effects of forest disturbance.

1.3. Butterflies as indicators of forest disturbance

Butterflies have been suggested as potentially excellent environmental indicators in temperate (Erhardt and Thomas 1991) and tropical regions (Brown 1991, Gilbert 1984, Kremen 1992). The larval stages of the majority of butterfly species are phytophagous, being entirely dependent on specific host plants. The exception to this is found within the Lycanidae family where a range of aphytophagous larval feeding has been reported. Throughout their lifetime as larvae, feeding as larvae on lichens, or algae and fungi, or in some cases only aphytophagous in later instars, feeding on ant larvae or on the secretions of Formicidae or Homoptera (Cottrell 1984). The majority of butterflies being phytophagous on specific hostplants, this specificity ranging from monophagy to oligophagy to polyphagy (in a few cases), closely links butterflies with the specific vegetation of the habitat. Keeping this plant-insect association intact, however, does not alone guarantee survival of a species. The county of Suffolk, England, has lost 42 % of its butterfly species this century, yet none of their foodplants have disappeared (Thomas 1989). Until 1979, when it bacame extinct in Britain, the large blue butterfly *Maculinea arion*, was found in several sites in south-west England in mutualistic association with the ant *Myrmica sabuleti*. Many of these sites were lost to agriculture, urbanisation or quarrying, or were undergrazed by wild and domestic herbivores, causing a large reduction in the ant, which in turn resulted in the demise of the butterfly (Thomas 1980).

As adults, tropical forest butterflies have been known to use a vast range of food sources including nectar, pollen, rotting fruits, tree sap, fungi, carrion, dung and urine. Reproduction in most kinds of butterflies is thought to be restricted by the amount of nitrogenous reserves accumulated during larval feeding (Engelmann 1970, Wigglesworth 1972). The majority of butterfly species feed on floral nectar and thereby obtain sugar to provide metabolic energy. For these butterflies, larval reserves are the major, if not only, source of nitrogenous materials available for egg

production. As an adult female, the number of eggs to be laid is thought to be a finite number detremined by the quantity of nutrients accumulated during larval feeding (Dunlap-Pianka *et al.* 1977, Engelmann 1970). This general life pattern does not hold for several groups of butterflies. A number of the Heliconius group of butterflies have evolved to utilise the nitrogenous components of pollen into their diet (the phylogenetically older members of this group not being able to do so), which has been found to be incorporated into egg production (Boggs 1981, Boggs and Gilbert 1979, Boggs *et al.* 1981, Gilbert 1972), and to extend the lifetime of individuals in this group to several months. Several ithomiid species of butterflies, primarily females, follow foraging army ant *Eciton burchelli* (Hymenoptera: Formicariidae) swarms and feed on ant-bird droppings (Ray 1980). It is beleived that they are using uric acid or partly digested proteins as a source of nutrients essential for egg production (Dunlap-Pianka *et al.* 1977, Gilbert 1972). Some ithomiine species are able to live at least 4 months (Gilbert 1972). Rotting fruits are used by about a tenth of the Trinidad butterfly fauna, and it is felt that perhaps this is a very rich source of carbohydrate compared with flower nectar (DeVries 1987). Carrion such as fish and meat are also excellent sources of proteins and used by the fruit-feeding group of butterflies. The fruit-feeding Satyrinae subfamily have also been reported to feed on fungi associated with decaying matter (DeVries 1987). A *Cissia penelope* (Satyrinae) individual was observed feeding on a cluster of small unidentified white bascillus fungi for over an hour in Trinidad, although it could not be confirmed that the butterfly was feeding directly on fungal tissue as opposed to rainwater which may have collected on them, for example (*personal observation*).

The males of several migrating butterfly species such as the Pierids, *Aphrissa statira* and *Phoebis argante*, and the Nymphalid "daggerwing", *Marpesia chiron*, are frequently found 'drinking' at puddles; a behaviour known as "puddling". A "puddle club" may comprise hundreds of individuals of several species, all of which are males. The first experimental work on puddling behaviour was carried out in the Amazon Basin (Colenette and Talbot 1928). They showed that males were attracted to the salts

from sweat. Later, sodium salts were demonstrated to be attractive to North American species (Arms *et al.* 1974). Minerals such as magnesium and sodium salts are obtained from urine pools, dung and road and river-side puddles.

The adults' roles as pollinators of plants through their nectar and pollen feeding, also link butterflies closely to the diversity and health of their habitats (Ehrlich 1984). Butterflies are also very sensitive to changes in temperature, humidity and light levels, parameters that are typically affected by habitat disturbance. Butterfly taxonomy is also well known when compared with other tropical insect groups and many species can be reliably identified in the field.

The disturbance of forest provides a rich mosaic of microhabitats varying in light and abiotic conditions, attracting secondary-growth, light-loving butterflies from the forest edge (DeVries 1988, Lovejoy *et al.* 1986). Work in forest fragments in Manaus, Brazil, showed a dramatic increase in butterfly species richness in forest habitats with increased light levels in the understorey, such as in large internal clearings and fragments which were semi-isolated (increased proportion of edge habitat), compared with inside forest (Brown 1991). These results have parallels in temperate forest habitats where the management of forest and rides to provide a large range of shade levels, has been found to increase the number of habitats suitable to different butterfly species (Warren 1985). Workers in Spain (Baz and Garcia-Boyero 1995) discovered a significant correlation between the species diversity of butterflies and woodland area, diversity increasing as the area and patchiness of the forest fragment increased. This increased patchiness with increased forest fragment area was the result of decreases in certain structural variables (cover, horizontal diversity and complexity) of the habitats (Baz and Garcia-Boyero 1995). Spitzer *et al.* (1997), working in montane forest in northern Vietnam, found that although butterfly species richness and diversity was higher in gaps, the conservation value of the closed canopy habitat lay in the presence of species with restricted ranges (Spitzer *et al.* 1997). Work with butterflies on Sumba, Indonesia, report similar findings, with those species occurring at highest

densities in secondary forests having wide geographic ranges and those at highest densities in undisturbed primary forest having restricted ranges of distribution (Hamer *et al.* 1997).

Smaller Costa Rican forest fragments have been found to contain depauperate butterfly faunas, whereas the species richness of nocturnal moths was found to be similar in all fragments and even pasture (Daily and Ehrlich 1996). This difference between butterflies and nocturnal moth species richness is best explained by movements of moths at night when ambient conditions in forest and pasture are most similar. Butterflies face substantial daytime temperature, humidity and solar radiation barriers (Daily and Ehrlich 1996).

With the development of new techniques, the inaccessible canopies of tropical rainforests have in recent times become much more accessible to study. Work in a Bornean rainforest revealed that 70 % of the forest's insect fauna was found in the soil and leaf litter, and as much as 28 % was found in the canopy (Stork 1988). Substantial fractions of the total butterfly fauna at tropical sites are found in the canopy (DeVries 1988). Butterflies in the fruit-feeding Nymphalidae guild appear to be stratified into canopy and understory species (DeVries 1988).

Another factor that must be taken into account when considering the determinants of butterfly abundance at a local spatial scale, including its susceptibility to extinction, is the relationship between local abundance of a species and geographic range size. The extinction of the large blue *Maculinea arion*, mentioned earlier, had a restricted range in Britain, which was finally whittled down to nothing. It was probably significant that the last remaining British populations recorded before its extinction were also on the margin of the butterfly's overall range, where conditions were possibly suboptimal for one link in the mutualistic chain (Samways 1994). When the butterflies inhabitating the wet lowlands of Costa Rica were studied, it was found that species with narrow geographic ranges were less able to make use of human-modified

environments than more widely distributed species (Thomas 1991). This bodes grave consequences for endemic butterflies restricted to unmodified habitats in light of the present rate of tropical forest destruction, which is more likely to affect endemic butterflies adversely. Following this trend of increased forest removal and increased levels of endemics disappearing, butterfly faunas of different areas will tend to become more and more alike, consisting of mainly generalist and geographically widespread species.

1.4. Objectives

This thesis explores the use of sampling and analytical methods to study the effects of forest disturbance, using butterflies as an indicator group of forest disturbance.

1.4.1. Main objectives

1) to investigate the effects of forest disturbance using components of habitat's butterfly assemblages as an indicator of forest disturbance.
2) to use several different methods to characterise the level of forest disturbance.
3) to use mark-release-recapture (MRR) techniques on fruit-trapped individuals to investigate temporal and spatial movements and in estimating population size.

1.4.2. Methods used to carry out objectives

The main objectives were acheived using the following methods:

1) this was studied at three different spatial scales:

(a) the comparison of butterfly assemblages of several habitats which varied in their disturbance histories,

(b) the effect of breaks splitting a single undisturbed habitat to the movement of fruit-feeding butterflies and

(c) the effect of gaps created by the selective extraction of single trees within habitats left to recover after logging for different periods of time. This was acheived using empirical data from one or both of two butterfly sampling methods, walk-and-count transects and fruit trapping.

2) This included two vegetation sampling methods and two photographic methods of obtaining measures of forest canopy openness.

3) MRR was used to:

(a) track individuals spatially to obtain information on movement patterns with respect to breaks between forest blocks, which may act as barriers to dispersal and thus species survival with increased forest fragmentation.

(b) track individuals temporally to uncover the lengths of time individuals of species remained resident in habitats.

(c) estimate population sizes of the more abundant species.

1.4.3. Thesis structure

Chapter 2 describes the study sites and butterfly sampling methods used in this thesis. Chapter 3 introduces the main thread of this thesis, the thread of forest disturbance and its effects on a habitat's butterfly assemblage. It investigates the butterfly assemblages of habitats as a whole using both walk-and-count and fruit trapping techniques (in the canopy and understorey), and compares the findings in pairs of forest habitats which are disturbed and undisturbed. Chapter 4 focusses on one undisturbed forest habitat and the effect of breaks between large blocks of forest to butterfly movements, and horizontal distribution patterns of species from a forest edge. Chapter 5 explores the polycyclic selective logging practice of the Periodic Block System (PBS) and in particular the component of the fruit-feeding guild of butterflies in tree gaps (0, 5 and 30 years after logging) and non-gaps in the same forest habitats. Chapter 6 investigates population parameters of several of the more abundant fruit-feeding

species encountered in Study 1 and 2 of Chapter 4, such as residency time and population size estimates. The last data chapter (Ch.7), examines the *Cissia* group of butterflies at a community ecology level, investigating aspects such as dominance and the relationship between mean local abundance and range size (both in terms of number of sites occupied and at the wider spatial scale of geographic range size). A general discussion, pulling together threads from the thesis as a whole is presented in Chapter 8.

Chapter 2

Study sites and butterfly sampling methods

2.1. Trinidad and its origins

Trinidad is an ideal locality for the study of Neotropical butterflies, containing a well documented butterfly fauna of over 600 species (Barcant 1970), representative of the species found in mainland South America. A comparison of the percentage of species found in each family compared with the total number of species, for Trinidad, Venezuela (separated from Trinidad by only 11 km across the Gulf of Paria) and the whole Neotropical fauna, reveals remarkable similarity between the faunas (Table 2.1).

Table 2.1. Proportions of species of the total butterfly fauna represented by families and subfamilies in the three regions, Trinidad, Venezuela and the Neotropical region as a whole (data taken from Beccaloni 1995) (Beccaloni and Gaston 1995).

Butterfly subfamily	Trinidad	Venezuela	Neotropics
Hesperidae	37.34	23.75	28.08
Papilionidae	2.44	2.16	1.85
Pieridae	4.38	4.58	4.50
Lycaenidae	15.10	17.27	18.15
Riodinidae	17.37	23.75	18.22
Libytheinae	0.16	0.04	0.03
Nymphalinae	11.53	12.09	14.35
Satyrinae	3.90	6.47	6.97
Brassolinae	1.62	1.34	1.13
Morphinae	0.16	0.91	0.77
Heliconiinae	2.44	1.81	0.91
Acraeinae	0.33	0.39	0.63
Danainae	0.65	0.35	0.13
Ithomiinae	2.60	5.10	4.30
TOTAL NO. SPECIES	616	2316	7179

The island of Trinidad is roughly rectangular in shape measuring c. 56 by 77 km (Fig.

2.1). Three mountain ranges traverse the island. The Southern Range consists of a series of low rolling hills extending along the south coast from Erin to Guayaguayare. Most of the hills in this range are only 60-90 m high, but in its eastern portion, the Trinity Hills rise to 300 m. There are two seasons per year, a dry season extending from January to May, and a rainy season from May to December. Rainfall varies from between 1650 mm and 2500 mm per year. Cumulative rainfall data (Fig. 2.2) over the relevant study periods in each year are shown for 1994 (data kindly supplied from three of the Trinidad and Tobago Water Resources Authority stations in southern Trinidad), 1995 (rain gauge outside field station in Guayaguayare) and 1996 (rain gauge in open at edge of B1 in Catshill). Temperatures in any year rise to a maximum of 35 ^{o}C and drop to a minimum of 15 ^{o}C.

The rich diversity of flora and fauna found in Trinidad, compared with other islands in the Lesser and Greater Antilles, has been put down to its recent break from continental South America, approximately 10, 000 years ago. The islands of the Greater Antilles (Cuba, Hispaniola, Puerto Rico and Jamaica), on the other hand, probably represent a former unsuccessful land-bridge between the two American continents. This early land bridge was broken into the large islands which now border the northern Caribbean sea, as the Caribbean plate moved eastwards (Comeau 1990-1991). The present land-bridge was actually formed about 800,000 years ago, and is likely to have been completed by the closure of a shallow connection through southern Nicaragua by volcanic accretion and structural uplift (B. van Wyk de Vries, pers comm.). The Lesser Antilles island arc developed along a subduction zone where the Caribbean plate collided with the Atlantic Ocean portion of the North American plate, and had formed sometime before 45 million years ago. The island of Tobago was still connected to Trinidad by a land-bridge until at least 14,000 years ago when the ice-sheets started retreating in North America and Europe. It was not until the start of the Holocene epoch (most recent geologic age, 10,000 years ago to the present), that the final land separation between Trinidad and South America occurred (Comeau 1990-1991).

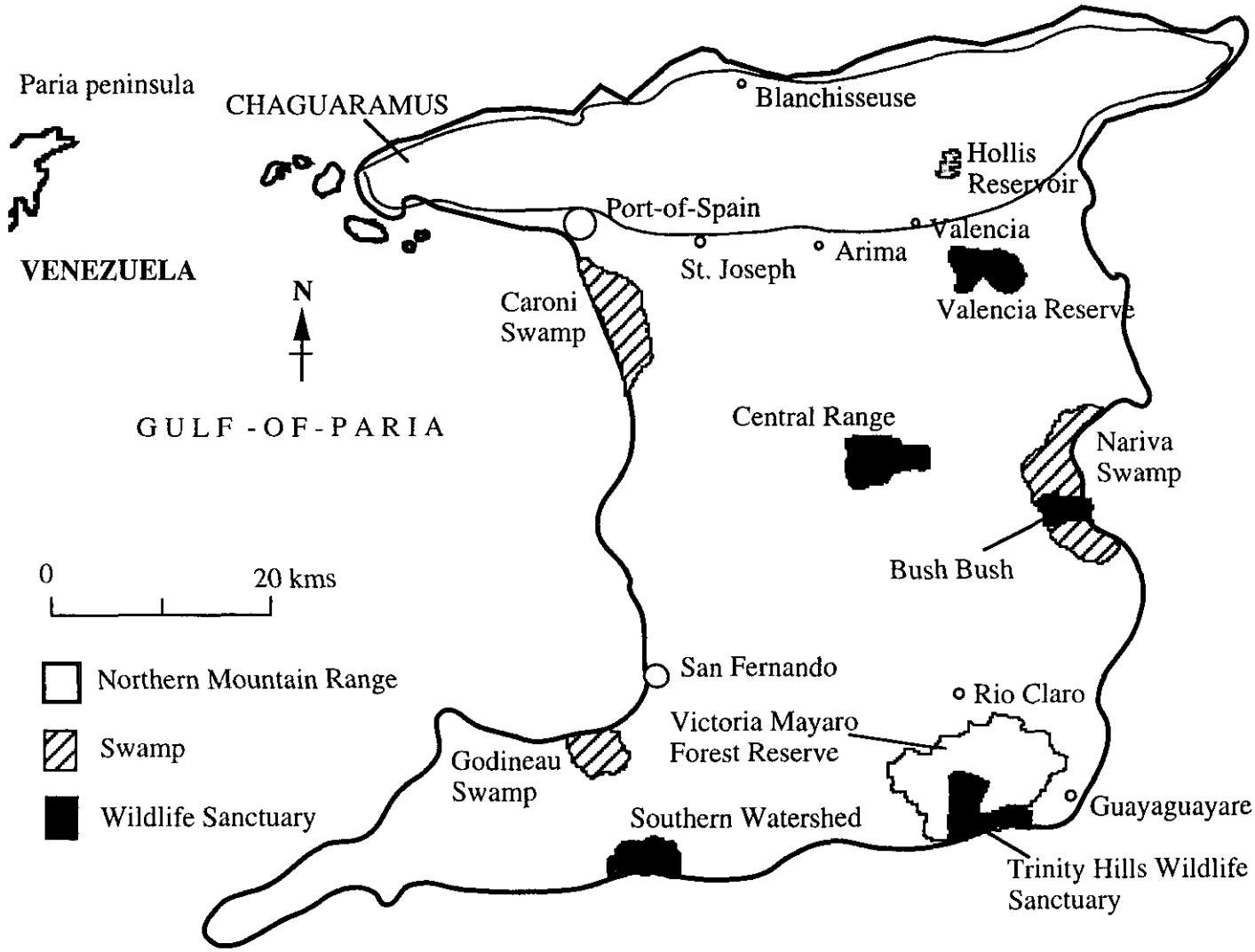


Figure 2.1. A schematic map of the island of Trinidad, showing its main forest reserves

Trinidad's earliest fossil plant records are from the Early Pleistocene, 1.8 million years before present day (mybp), and represent a flora indicative of a moist evergreen forest similar to the seasonal evergreen forest of today (Beard 1946). Land in Trinidad probably occurred above sea-level in the Early Miocene (22 mybp) and may even have appeared as early as the Middle Oligocene (30 mybp). Prior to this, sediments forming Trinidad were entirely below sea-level. Once emerged, this Northern Landmass of folded Cretaceous sediments, consisting of what is now the Northern Range of Trinidad, Tobago, the Sierrania de la Costa of northern Venezuela and Magarita, may well have been separate from the mainland, but by the Middle Miocene (14 mybp), it was attached to the continent. It presumably then supported vegetation of A continental nature. By the end of the Miocene (5 mybp), the Central Range of Trinidad was above sea-level, and by the Middle Pliocene (3 mybp) all of Trinidad, including Tobago, formed part of the Orinoco Delta apart from the Trinity Hills, which were elevated above sea-level during the Early Pleistocene (1.8 mybp).

It is likely that a moist tropical forest flora (which has existed since 30 million years ago, the same time that Trinidad first appeared above sea-level) was found in Trinidad up to the start of the Pleistocene (1.8 mybp). Fluctuating climate, including eight glacial maxima in the last million years, however, are likely to have caused fluctuations in vegetation cover in Trinidad as found in other tropical regions. During drier periods deciduous forest and climatic savannas spread. A 20 % drop in rainfall in the tropics at the time of maximum glaciation would cause a spread of arid conditions into strongly seasonal climatic regions like Trinidad (Colinvaux 1989).

Recent maximum forest cover in Trinidad is likely to have existed since the optimum post-glacial climatic period between 7,000 and 5,000 years ago, and more or less persisted until pre-Columbian times (500 ybp). It has been estimated that whereas in 1989, about 20 % of Trinidad's land area was covered in seasonal evergreen and 3 % in semi-evergreen forest, in pre-Columbian times these respective figures were 75 % and 10 % (Beard 1946, Comeau 1990-1991).

An analysis of aerial photographs, carried out during the 1978-1980 forest inventory, covered most but not all of the country and showed the following forest types and areas of coverage: evergreen seasonal forest - 115,200 ha; semi-evergreen seasonal forest - 14,100 ha; swamp forest - 16,400 ha; montane forest - 22,500 ha; dry evergreen seasonal forest - 500 ha; deciduous seasonal forest - 3,700 ha; plantations, including non-timber - 21,400 ha; and secondary forest - 6,000 ha; totalling 199,900 ha (Synnott 1989). Due to an incomplete aerial survey, this total area of forest coverage is likely to be an underestimate, and hence is less than the figure given in Synnott's report (1989) of 272,800 ha (54,400 ha being private and 218,400 ha being state-owned), or 53 % of Trinidad's 512,400 ha land area. This figure originates from Forestry Division estimates. Of this forest land, 126,700 ha are designated as Forest Reserves (FRs), with 94,500 ha being Production FRs and 32,200 ha being Protection FRs. About 75,000 ha of natural forest are intended for long-term sustainable timber production, of which 16,000 ha have been classified as intensively managed, meaning that they have been logged and then closed until the next cycle, as of 1989 (Synnott 1989). The most recent FAO estimates (FAO 1997) of the percentage of Trinidad's land area covered in forest are 34 % (174,000 ha) in 1990 and 31.4 % (160,894 ha) in 1995, as opposed to the 53 % (272,800 ha) cited above.

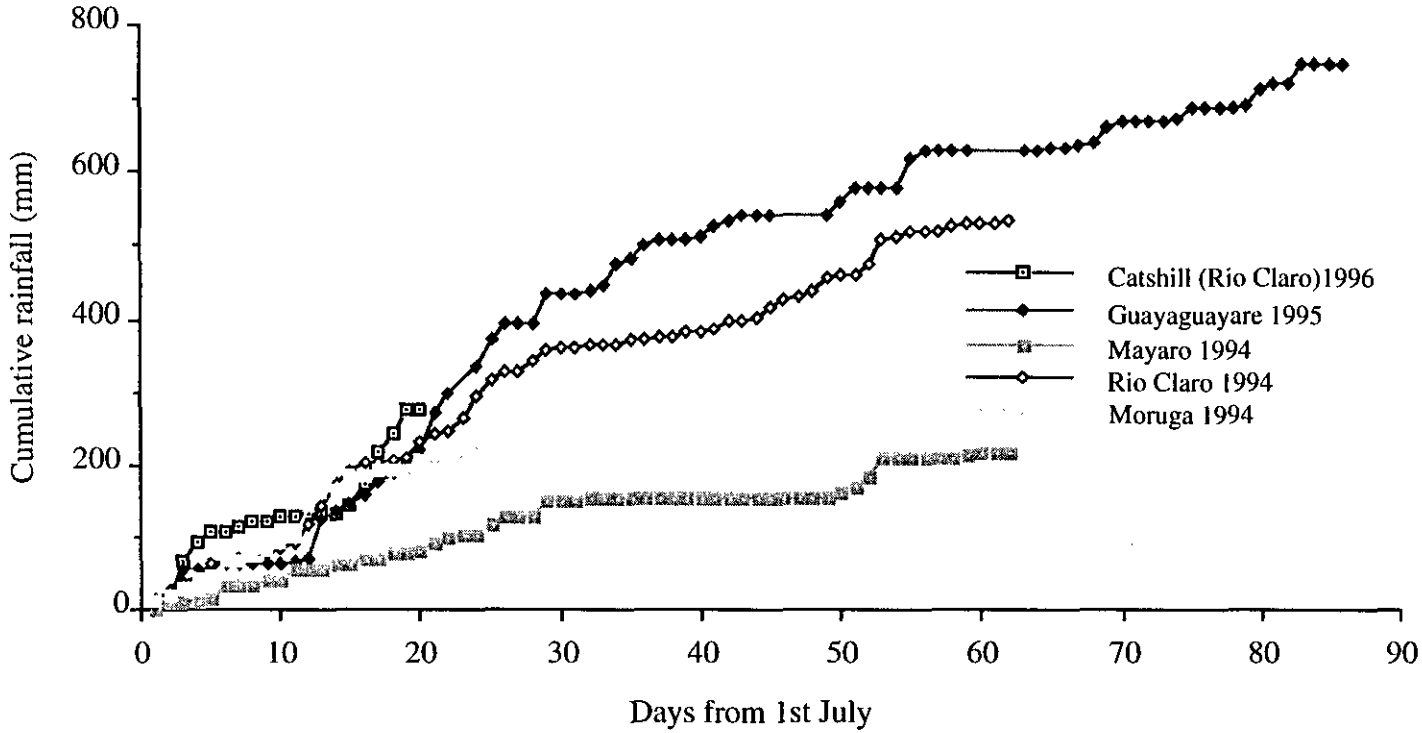


Figure 2.2. Cumulative rainfall (mm) for 3 sites in 1994 (WRA, Trinidad & Tobago), 1995 (Guayaguayare) and 1996 (Catshill)

2.2. Study sites

Four study sites (Fig. 2.3) were used to undertake the research for this thesis. Three of these sites are within the Victoria Mayaro Forest Reserve and one falls just outside its boundary. A large portion of the 52,000 hectare Victoria Mayaro Forest Reserve (Fig. 2.3) is seasonal evergreen forest dominated by *Mora excelsa* Benth. (Leguminosae). Further south the forest becomes drier and semi-evergreen, dominated in the canopy by *Carapa guianensis* Aubl. (Meliaceae) and *Pentaclethra macroloba* (Willd.) Kuntze (Leguminosae) (Beard 1946).

Ch. 3 explores characteristics of butterfly assemblages within pairs of forest habitats where one habitat is undisturbed and one is disturbed. The first pair of undisturbed and disturbed forest habitats described below are seasonal evergreen forests, and the other pair are seasonal semi-evergreen forest (Beard 1946). Ch. 4 investigates butterfly distribution relative to a forest edge and movement patterns across breaks in the forest. This was carried out in the undisturbed semi-evergreen forest, close to the field station. Ch. 5 examines the fruit-feeding butterfly fauna of gaps versus non-gaps in Blocks of selectively logged forest of different ages since logging. This is the disturbed evergreen forest. Ch. 6 uses data from Ch. 4 to analyse elements of the population structure of several species, hence this Chapter, like Ch. 4, is also based in the undisturbed semi-evergreen forest. Ch. 7 investigates aspects of community structure of the *Cissia* group of butterflies using data from all four of the study sites described here.

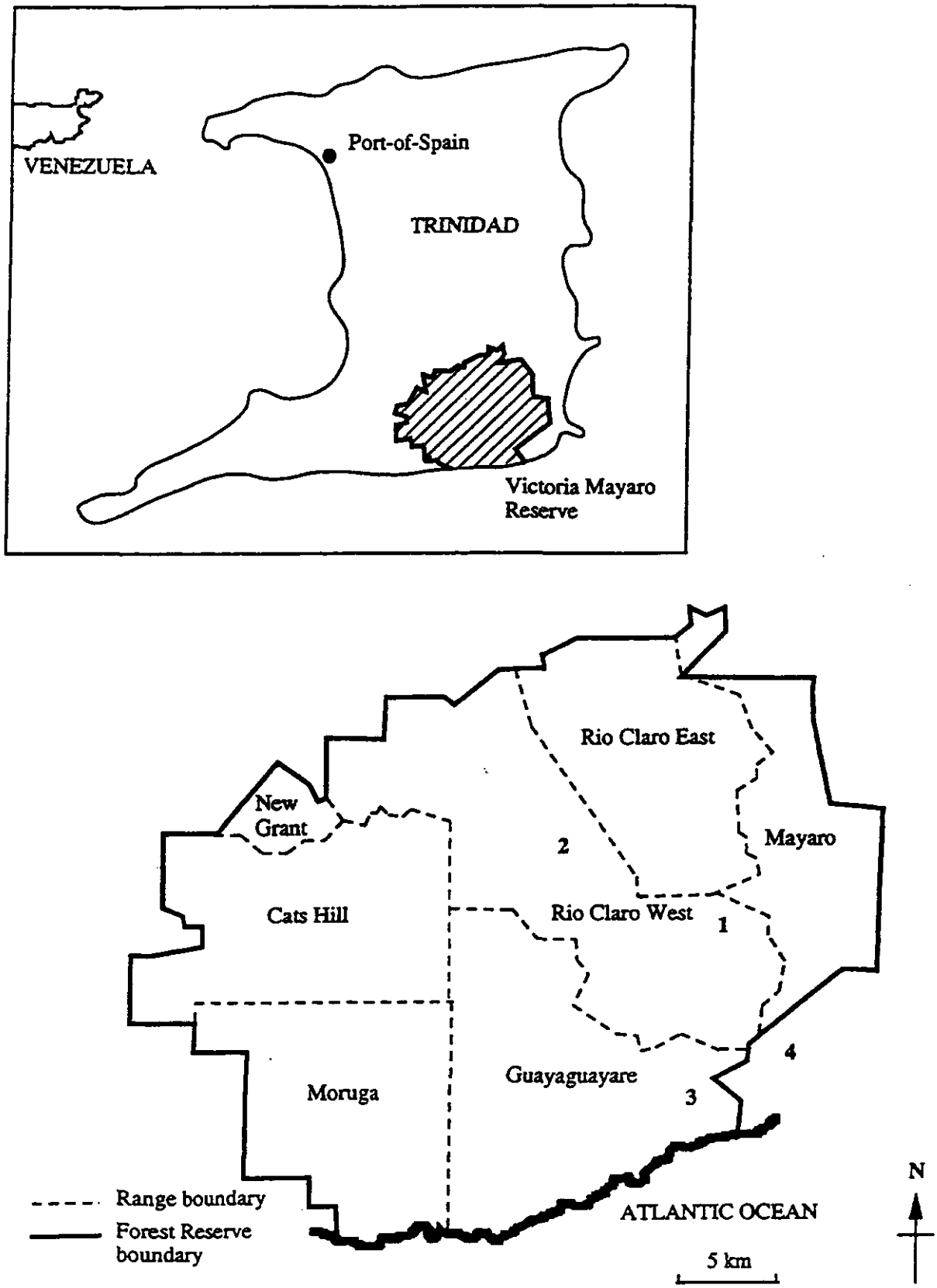


Figure 2.3. A map of Trinidad showing the Victoria Mayaro Reserve and the four forest habitats studied: evergreen undisturbed (1) and disturbed (2) and semi-evergreen undisturbed (3) and disturbed (4).

2.2.1. Evergreen forest: undisturbed (PSP80)

This undisturbed evergreen forest study site was set in a Forestry Division Permanent Sampling Plot (PSP80) set up in 1983. These are the only PSPs established in tropical forest in America as part of a statistically designed sampling programme for forest management rather than as a research study (Synnott 1989). PSP80 is located just north of the junction of Vietnam Road (Exxon oil company private road) and Spring Lizard Road which leads from the Petrotrin oil compound to Rio Claro. As both of these roads are oil company roads with security guards at control gates, the forest here was well protected from squatting and over-exploitation by hunters. Unfortunately, sometime after Exxon left in 1995 or 1996, part of this primary forest habitat used in 1994 was badly damaged by fire.

The forest is evergreen seasonal forest dominated by *Mora excelsa*, a tree species that can make up to 85-95 % of the individuals forming the forest canopy (Clubbe and Jhilmit 1992). Other species that reach the canopy layer are *Carapa guianensis*, *Terminalia dichotoma* (G.F.W) Meyer, *Pterocarpus rohrii* Vahl. and *Spondias mombin* L. The middle story is typically dominated by *Pentaclethra macroloba*, *Pachira insignis*, *Sterculia caribaea* R.Br. and *Clathrotropis brachypetala* (Tul) Kleinh. The understorey is composed of *Swartzia pinnata* Willd., *Brownea latifolia* Jacq. and the three palm species *Sabal mauritiformis*, *Euterpe langloisii* Burrett and *Maximiliana maripa* (Beard 1946, Clubbe and Jhilmit 1992).

2.2.2. Evergreen forest: disturbed (Periodic Block System)

The evergreen seasonal forests of South-East Trinidad are logged using two different forest management techniques, the Open Range Method (ORM), and the Periodic Block System (PBS). The ORM was introduced in the 1920s and has been the system most widely used since the start of professional management in Trinidad and still operates in some forest reserves (e.g. the Valencia Range). The only control exercised on ORM is a girth limit for certain species.

The ORM was also employed in marked out blocks of forest in the Catshill Range in 1954, but by 1960 it became a PBS, a sustained-yield selection system with a cutting cycle of 30 years. The PBS is based on a set of tree selection procedures, which includes for example, not removing all the straightest, most well-formed boles (which over time will deplete the gene pool of tall straight-boled forming trees) and leaving numbers of large fruiting trees such as hogplum,*Spondias mombin*, which although an economically important species, also has a high wildlife value, hogplums being a food source for many wildlife species. Under this polycyclic management regime, one block of forest is opened each year, on a 30 year rotation cycle. Of the 30 Periodic Blocks (approximately 165 hectares or 400 acres each in size), four were investigated in the course of this thesis work. These were Block 4 (B4) which was logged in 1993 and sampled in 1994 (1 year after logging), B6 which was logged and sampled in 1996 (0 years after logging), B1 which was logged in 1991 and sampled in 1996 (5 years after logging) and B7 which was sampled in 1996 and last logged in 1966 (30 years after logging). Apart from B7, all the Blocks were on their second rotation.

2.2.3. Semi-evergreen forest: undisturbed (Trinity Hills Wildlife Sanctuary)

Trinity Hills Wildlife Sanctuary was established in 1934 and is the largest wildlife reserve in Trinidad (Bacon and Ffrench 1972) and the second largest designated protected area covering 6486 hectares (IUCN 1992). It lies within the Victoria Mayaro Forest Reserve (Fig. 2.1) on the south coast. The sanctuary has been under mining lease to private and state-run oil companies for at least 30 years. A state-run enterprise, the Petroleum Corporation of Trinidad and Tobago Limited has had the lease of the sanctuary since 1988. According to Chapter 67:01 of the Conservation of Wild Life Act (Government of Trinidad and Tobago, 1963), wildlife sanctuaries are protected from encroachment, agricultural expansion, logging, cattle grazing and hunting wild animals. Game species such as agouti *Agouti paca*, red brocket deer *Mazama americana* and collared peccary *Tayassu tajacu* can be hunted legally, species such as

the red howler monkey *Alouatta seniculus insulanus* and white-fronted capuchin monkey *Cebus albifrons* are protected by law (Laws of Trinidad and Tobago 1963).

The study site was set up in the forest at the south-eastern boundary of the sanctuary. This forest is seasonal semi-evergreen forest of the crappo (*Carapa guianensis)* - guatecare (*Eschweilera subglandulosa*) association (Beard 1946). *Pentaclethra macroloba* is the dominant tree of the canopy layer and throughout this forest type the characteristic palm, and most abundant understorey plant, is *Sabal mauritiformis* (Karst.) Griseb. The commonest large trees in decreasing dominance are *Carapa guianensis* and *Pachira insignis* (SW) Sav., *Eschweilera subglandulosa* (Steud) Miers., *Trichilia smithii* C. DC., *Crudia glaberrima* (Steudel) Macbr. and *Guarea guara* (Jacq.) P.G. Wilson (Beard 1946).

2.2.4. Semi-evergreen forest: disturbed (Guayaguayare)

Guayaguayare is a small fishing village situated on the south-eastern peninsula of Trinidad. A Wildlife Section house in the Petrotrin oil compound was used as the base for these studies, offering easy access to the four study sites (Fig.2.3). The study habitat was situated in the disused cocoa estate behind the house which was originally part of the St. Mary's estate, part of which is still in operation today, cultivating cocoa and coconuts. This forest is of the semi-evergreen seasonal forest type (Beard 1946) dominated by *Pentaclethra macroloba* and *Erythrina* sp., which shade the cocoa (*Theobroma cacao*). *Zanthoxylum* sp. and *Hura crepitans* L. as well as several palm species such as *Maximiliana maripa* (Aubler) C. Martin and *Sabal mauritiformis* are are also well-represented in this habitat. A large swathe of Zingiberales (*Heliconia*, *Strelitzia* and *Zingiber* species) skirts the forest edge and numerous ditches and hollows soon fill up with water after rain.

2.3. Butterfly sampling

Studies were conducted in the early wet season after the remarks of Barcant (1970) that the best time for collecting butterflies in Trinidad is at the onset of the wet season rains, when many species emerge from their dry season diapause. A peak in insect abundance at the end of the dry and beginning of the wet season was also found at Cocha Cashu in Peru using ultra-violet light traps (Janson and Emmons 1990). The total weight of insects collected were dominated by Orthoptera, Coleoptera and Lepidoptera. In his study on butterfly stratification between the forest canopy and understorey, DeVries (1988) conducted his work at the end of the wet season, "a time when butterfly abundance is low". In contrast, Emmel and Leck (1970) found that for butterfly species in a large clearing in Barro Colorado Island, Panama, the peak number of species flew in the transitional period between the end of the wet season and the start of the dry season.

Two methods of collecting butterfly abundance information were used in this study. These were walk-and-count transects, and fruit traps placed in both the understorey and the canopy. More detailed information was collected on movements, longevity and absolute population size estimates using mark-release-recapture (MRR) techniques.

2.3.1. Walk-and-count transects

Transect routes were walked between 8.30 am and 10.30 am each morning and between 3.30 pm and 5.00 pm each afternoon (Emmel and Leck 1970). An initial pilot study into activity periods of fruit-feeding butterflies was undertaken in Ch.3.

Sampling was generally carried out morning and afternoon in four day blocks over the sampling period, unless it was raining or it had been raining up to one hour previously. In this case sampling was not carried out at all. All the butterflies seen 2.5 m either side or 5 m in front of the transect route (Cheverton and Thomas 1982, Hill *et*

al. 1995) were recorded. An individual was chased and caught wherever possible, for positive identification. If the individual could not be identified in the field, it was killed and collected for later identification. If an individual could not be caught then a description was noted and a tentative identification made. Killing specimens was acheived by placing the butterfly in a transparent envelope with the wings folded together above the body in the resting position. A record of the date, time, locality and species name (if collected as a voucher specimen) was written on the envelope which was then placed in a sealed tupperware tub with cotton wool and a few drops of ethyl acetate. Voucher specimens were collected and are presently housed at the Open University, Milton Keynes, to be later donated to the British Museum of Natural History (BMNH) in London. This walk-and-count transect method originates from methods used for the Butterfly Monitoring Scheme (Hall 1981, Pollard 1977) across Great Britain since 1976. Walk-and-count sampling of butterflies has also been carried out in the tropics (Cheverton and Thomas 1982, Hill *et al.* 1995).

A map of each transect route was made in case of future replicated walk-and-count sampling at the same sites (see Ch.3).

2.3.2. Fruit traps

The basic design of the sampling and fruit trap comes from work carried out in Costa Rica (DeVries 1987; DeVries 1988; DeVries, *pers.comm.*). The fruit trap (Fig. 2.4) consists of a cylindrical fine-net cage, closed at one end and supported each end by steel rings. An opening into the netting cylinder, closed by a zipper or velcro, allows butterflies to be extracted after capture. Commercial butterfly mating cages with the bottom cut out, proved ideal (from Butterfly Connections in Somerset, UK).

From the open end is suspended a flat piece of material to support rotting fruit. In 1994, the bases were 50 cm squares of 5 mm plywood, sealed by several layers of varnish. The plywood lasted the duration of the study period, but they were not re-

useable. 3mm thick foam PVC sheeting (Formerton Plastic Sheeting, Milton Keynes, UK) cut into 50 cm squares, however, lasted the 1995 and 1996 field seasons, and are still useable.

In each habitat studied, a number of locations were chosen where either or both a canopy (minimum of 10 m off the ground) and an understorey trap (1 m off the ground) were placed. The fruit traps in each habitat were baited, placed in the canopy or understorey and then generally run for four consecutive days, throughout a sampling period. The traps were baited the night before sampling began. Traps were inspected in the morning between 9.00 am and 11.30 am and in the afternoon between 3 pm and 5.30 pm every day during the trapping period. Traps were not sampled for butterflies in heavy rain, butterflies caught being ignored, although the condition of the bait was checked and restocked if necessary.

For individuals of species which could be identified in the field, their presence in the traps was recorded and they were marked and released. Otherwise they were collected as voucher specimens in 1994, but this was not necessary in 1995 and 1996. A wing-length measurement from the apex to the base of the forewing was taken for many individuals (Ch.4) and the distance flown on release also noted (Ch.4). Traps were located on walk-and-count transect routes whenever both butterfly sampling methods were used (Ch.3). Several of Trinidad's fruit-feeding butterfly species are shown in Plates 2.1 (*Cissia penelope*, *C. renata* and *C. libye*), Plate 2.2 (*Caligo teucer* and *Taygetis andromeda*) and Plate 5.1 (*Colobura dirce*). These species were studied to a greater or lesser degree in following chapters.

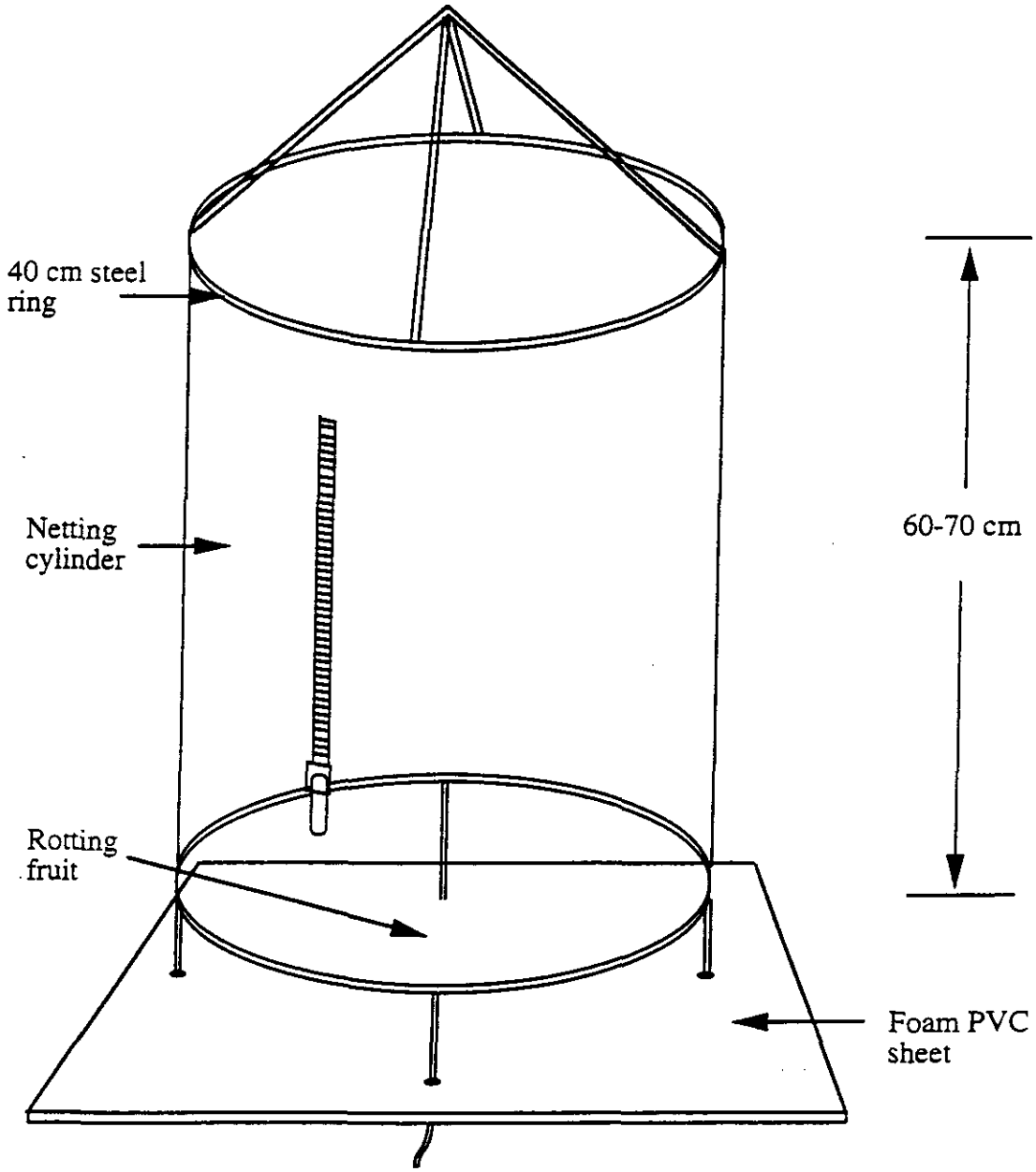


Figure 2.4. A butterfly fruit trap. Foam PVC bases were 5-10 cm wider than the diameter of the net cylinder to allow butterflies to settle before entering trap. The gap between the net cylinder and the base was about 6 cm. Traps were baited with rotting mango due to its wide availability and subsequently for continuity, although other fruits, carrion, faeces or fish can be used.

Plate 2.1. Three Satyrinae species in the *Cissia* group, *Cissia penelope* (top), *C. renata* (middle) and *C. libye* (bottom)

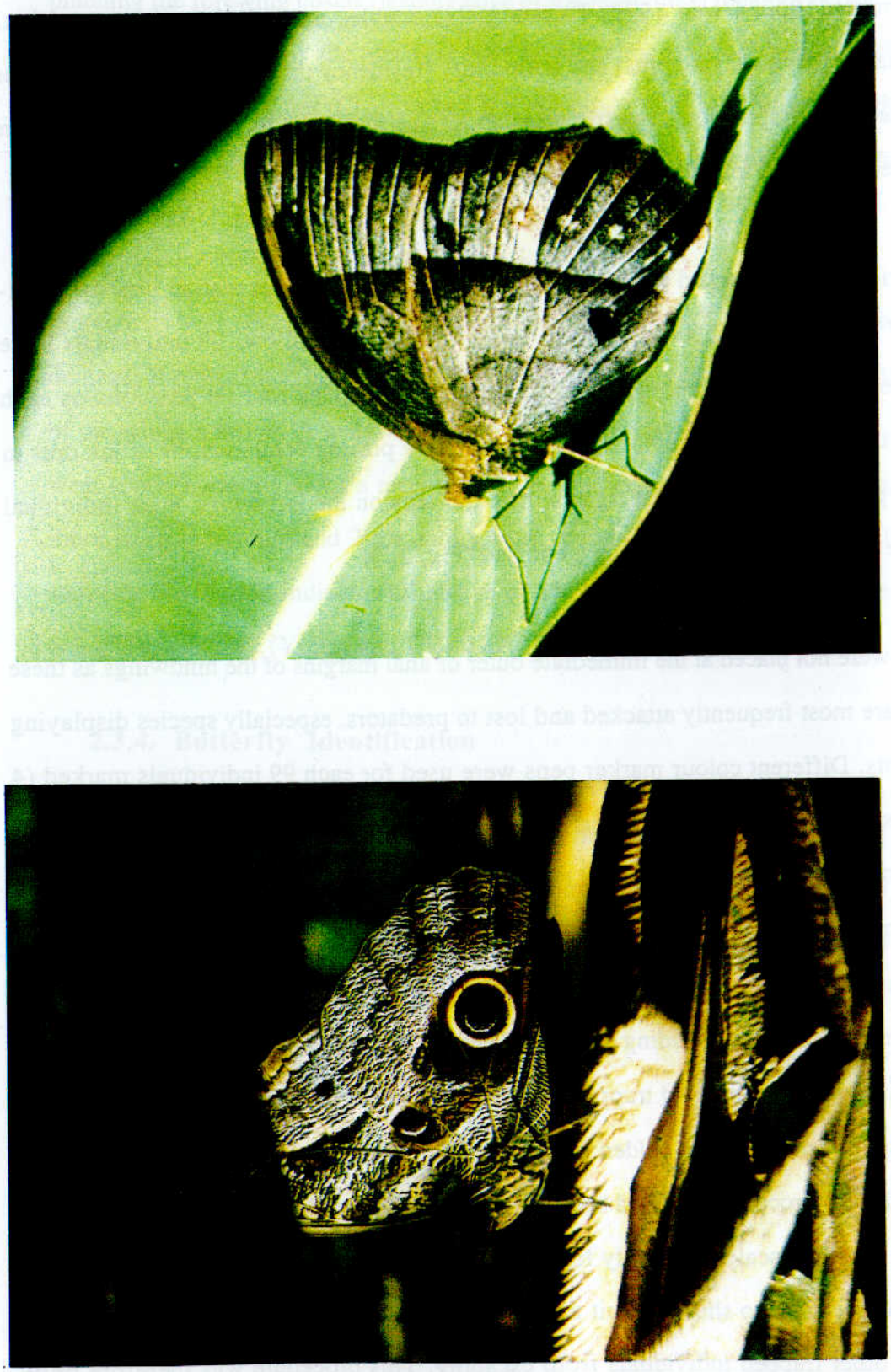


Plate 2.2. The cryptic "owl butterfly" *Caligo teucer* on the forest floor (left) and *Taygetis andromeda* (right)

2.3.3. Mark-release-recapture (MRR)

The use of this technique (Brussard 1971, Dowdeswell *et al.* 1940, Ehrlich and Davidson 1960, Owen 1975, Turner 1971) enables individuals to be traced both spatially (movement patterns) and temporally (residency time) throughout the duration of the study. Population size estimates can also be made (Ch.6). MRR techniques were carried out on all individuals caught in fruit traps.

Individuals were marked with a permanent Staedtler Lumocolor marker pen, using a 1-2-4-7 system (Ehrlich and Davidson 1960). This method allows 99 individuals to be marked with one coloured pen. This is acheived by having four set positions on each wing that represent the numbers 1, 2, 4 and 7. By placing combinations of ink dots in these positions, digits on the right wings and tens on the left wings, each individual can be uniquely marked and thus identified (Fig. 2.5).

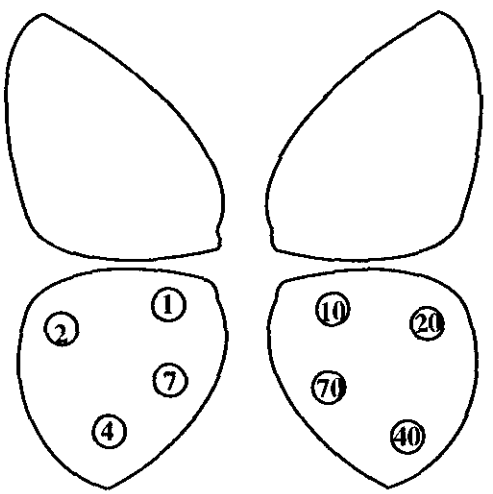
Spots were not placed at the immediate outer or anal margins of the hindwings as these areas are most frequently attacked and lost to predators, especially species displaying eyespots. Different colour marker pens were used for each 99 individuals marked (4 colours) and subsequently combinations of these colours. Individuals were handled for as short a time as possible to avoid excessive adverse handling effects (Morton 1982, Morton 1984, Singer and Wedlake 1981). In 1994 all individuals were removed from the fruit trap by capturing the butterfly under a small square plastic container against the side of the fruit trap, sliding a piece of netting over the top of the container before extracting the container and trapped butterfly out of the fruit trap. The butterfly was then trapped with its wings folded in the netting, marked through the netting and then released. This procedure avoided handling the butterfly and hence reduced the amount of wing damage (scales are easily lost by handling), but was time consuming. It also required assistance to shut the fruit trap each time an individual was being marked to prevent other trapped individuals from escaping. This procedure was therefore only used in 1994 when assistance was available and only 380 individuals were marked,

but not in 1995 and 1996 when more intensive fruit trapping was carried out with no assistance and more than 2000 individuals were marked each year. In this study all butterflies were removed from the fruit trap and held, as gently as possible, by pinching the forewing costas (leading edge of the forewings) together between thumb and forefinger. This is the sturdiest part of the wing and for species such as the *Archaeoprepona* species (Charaxinae), it is essential to hold the butterfly tightly near the base of the forewings or the individual will fly off leaving you holding the tips of its forewings !

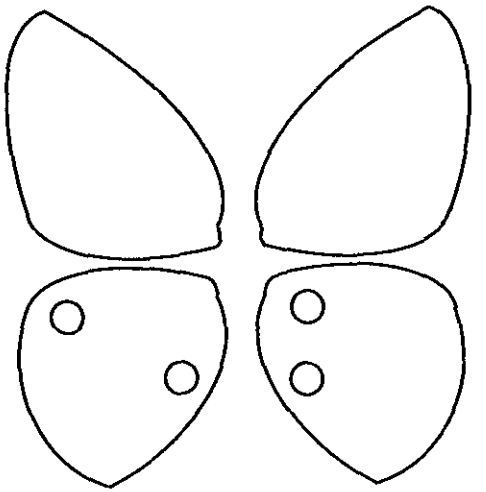
Individuals were also given a wing damage score from A to C, where A represented no damage; B represented up to about 25 % of the wings missing and C, more than 50 % of the wings missing. A wing wear score was also given, ranging from 0 to 2. Wing wear score 0 was given for a recently emerged butterfly in pristine conditon, 1 for a more worn individual and 2 for a very worn individual. Wing wear has often been suggested as a good indicator of the age of adult butterflies, with more wing scales being lost with time (Young and Thomason 1974).

2.3.4. Butterfly Identification

Butterflies in most families were identified using Barcant (1970) and DeVries (1987) in the field and the D'Abrera volumes on Neotropical butterflies (1981-94) at the University of the West Indies and in the UK. *Archaeoprepona* and *Prepona* species (Nymphalidae: Charaxinae) were identified using Papworth (1981).



1. The verso (underside) surface of a diagrammatic butterfly showing the spot positions for units (right hindwing) and tens (left hindwing)



2. The marks that represent the individual marked number 89

Figure 2.5. The 1-2-4-7 marking system used in the mark-release-recapture (MRR) procedure (from Brussard 1971).

2.3.5. Butterfly classification

In naming taxa in this thesis, I have concurred with the system employed by P.J. DeVries (1987) in his study of the butterflies of Costa Rica and Singer (1993) for the *Cissia* group. The systematics of butterflies in the Neotropics is still being unravelled today. Whereas classification of the Papilionidae and Pieridae are fairly straight forward in that apparent phylogenetic affinities are shown, within the Nymphalidae, component subfamilies, tribes and genera have not been examined for phylogenetic affinities. Hence the Nymphalidae must be viewed as a phylogenetically unstudied group of taxa composed of various classifications. The problem of arranging the Nymphalidae is an old one (Ackery 1984, Ehrlich 1958, Seitz 1907-1924). No one has analysed the nymphalids in detail below the subfamily level on a global basis, and so there is only a composite picture of their affinities.

Muller (1886), in DeVries' view, has produced the most useful classification of the Neotropical Nymphalidae. Although most modern authors ignore Muller's classification (Muller 1886), DeVries incorporates his overall framework for the arrangement of the Costa Rican nymphalid fauna, while adding modifications in the form of more modern generic or subfamilial revisions (DeVries 1987).

I have used DeVries (1987) nomenclature throughout this thesis, apart from the *Cissia*, *Eupthychia* and *Chloreuptychia* group of butterflies which I have all put in the *Cissia* genus, following Singer (1993).

Chapter 3

The effects of forest disturbance on butterflies using two sampling methods

"The butterfly is to be honored; by pollinating flowers it teaches children industry; by its beauty an appreciation of the natural world." (Zuni Pueblo Indian Wisdom).

3.1. Introduction

This Chapter describes work carried out to investigate and compare the butterfly assemblages found in pairs of forest habitats differing in disturbance level. The butterfly assemblages of each habitat were identified using two methods of sampling (Ch.2). The term 'assemblage' is used in this study to describe the suite of butterfly species encountered in each habitat by a sampling method. In this study, greater levels of disturbance had occurred at some time in the two disturbed habitats. One habitat had been disturbed and managed to grow cocoa and the other had been selectively logged under the PBS, one year prior to sampling.

A summary of the reported effects of tropical forest disturbance on the forest's flora and fauna (vertebrate and invertebrate), including butterflies, have been documented in Ch. 1.

The main objectives of the work described in this Chapter were:

1) to analyse the effects of forest disturbance on the composition of forest butterfly assemblages by sampling pairs of forest habitats differing only in disturbance level, so that one habitat was disturbed and one was undisturbed.

2) to compare the findings of the effects of forest disturbance on butterfly assemblages using two methods of butterfly sampling, walk-and-count (forest understorey) and fruit trapping (forest understorey and canopy).

3) to present a standardised method of quantifying the butterfly assemblage found in each habitat, allowing comparison between assemblages found in differently disturbed forest habitats.

3.2. Methods

3.2.1. Study sites

Butterfly populations were investigated in the semi-evergreen seasonal forest in southernmost Trinidad and the evergreen seasonal forest, further north in the Victoria-Mayaro Reserve (Fig. 2.3). Pairs of habitats were chosen in each forest type on the basis of differing management histories which were likely to have resulted in different levels of disturbance. Each habitat in a pair is referred to as disturbed or undisturbed. The undisturbed evergreen forest (Sec. 2.2.1) had no known history of management, whilst the disturbed evergreen forest habitat (Sec. 2.2.2) had recently been selectively logged. The undisturbed semi-evergreen forest was situated in the Trinity Hills Wildlife Sanctuary (Sec. 2.2.3) whilst the disturbed semi-evergreen forest, 3 km away, was a disused cocoa plantation (Sec. 2.2.4).

3.2.2. Butterfly sampling methods

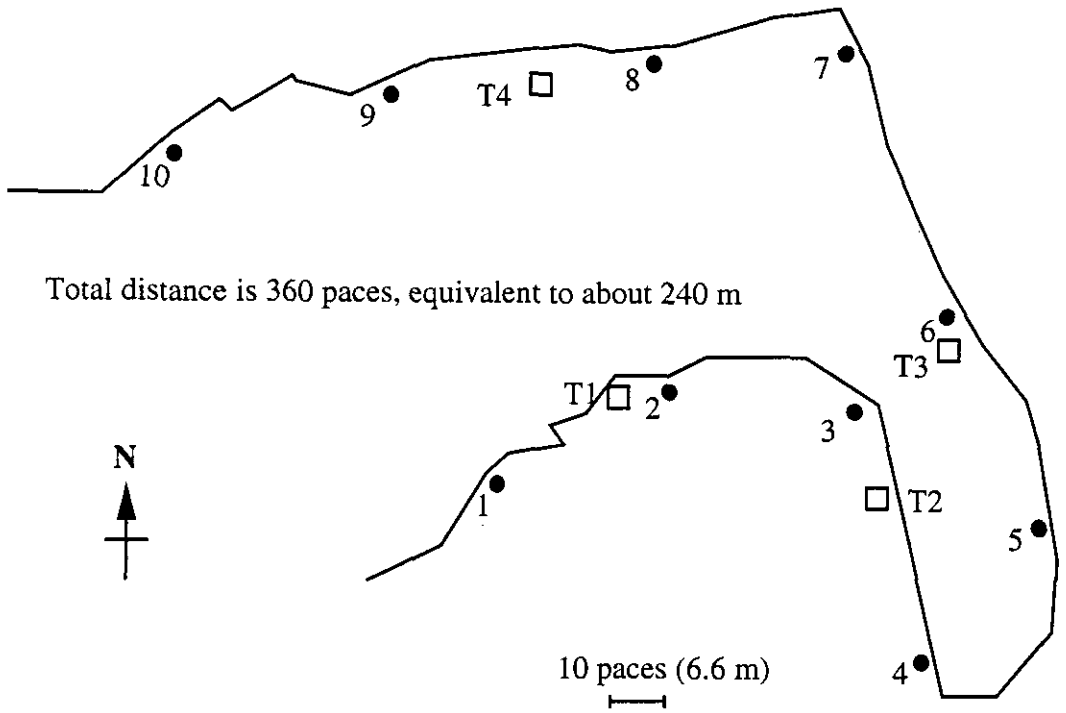
Two methods of collecting butterfly abundance information were used in each of the four habitats. These were walk-and-count transects, and fruit traps placed in both the understorey and the canopy positioned along the walk-and-count routes (see Ch. 2 for details of these methods). Walk-and-count transects were carried out for four consecutive weeks whereas fruit trapping was carried out alternately for one week in the understorey and one week in the canopy over the same four week period from 26th May 1994 to 18th July 1994 (Table 3.1). The use of fruit trapping techniques and walk-and-count butterfly methods ensured sampling of a wide spectrum of the forest butterfly fauna (Sparrow 1994) and allowed investigation of the stratification of the butterfly assemblage.

Table 3.1. Sampling timetable. Weeks when walk-and-count transects (____), canopy fruit trapping (----) and understorey fruit trapping (.....), were carried out in each forest type in both disturbed and undisturbed forest habitats.

	Week numbers commencing 26.5.94 - 18.7.94							
Habitat	1	2	3	4	5	6	7	8
Semi-evergreen	____	____	____	____				
	------	.....	------	.....				
Evergreen					____	____	____	____
					------	.....	------	.....

Within each habitat category, walk-and-count transect routes of approximately 30 minutes duration were undertaken. Due to differences in terrain and vegetation, this resulted in transects being of different lengths: 0.24 km (disturbed semi-evergreen, Fig. 3.1.a), 0.37 km (undisturbed semi-evergreen, Fig. 3.1.b), 0.46 km (disturbed evergreen, Fig. 3.2.a) and 0.55 km (undisturbed evergreen, Fig. 3.2.b). Transects were walked and mapped using a compass. Transect lengths were crudely measured using one person's 'normal' stride length, which was converted into metres. Inaccuracies in these measurements are inevitable as stride length is variable, especially with changes in topography. These transects were carried out between 08:30 and 10:30 each morning and between 15:00 and 17:00 each afternoon. Butterfly peak activity times (denoted by the maximum number of species and individuals observed in any hour's walk-and-count transect) was investigated by hourly walk-and-count transects conducted over a 12 hour period, in the disturbed semi-evergreen habitat.

a. Semi-evergreen disturbed (Guayaguayare) walk-and-count transect route 1994.



b. Semi-evergreen undisturbed (Trinity Hills) walk-and-count transect route 1994.

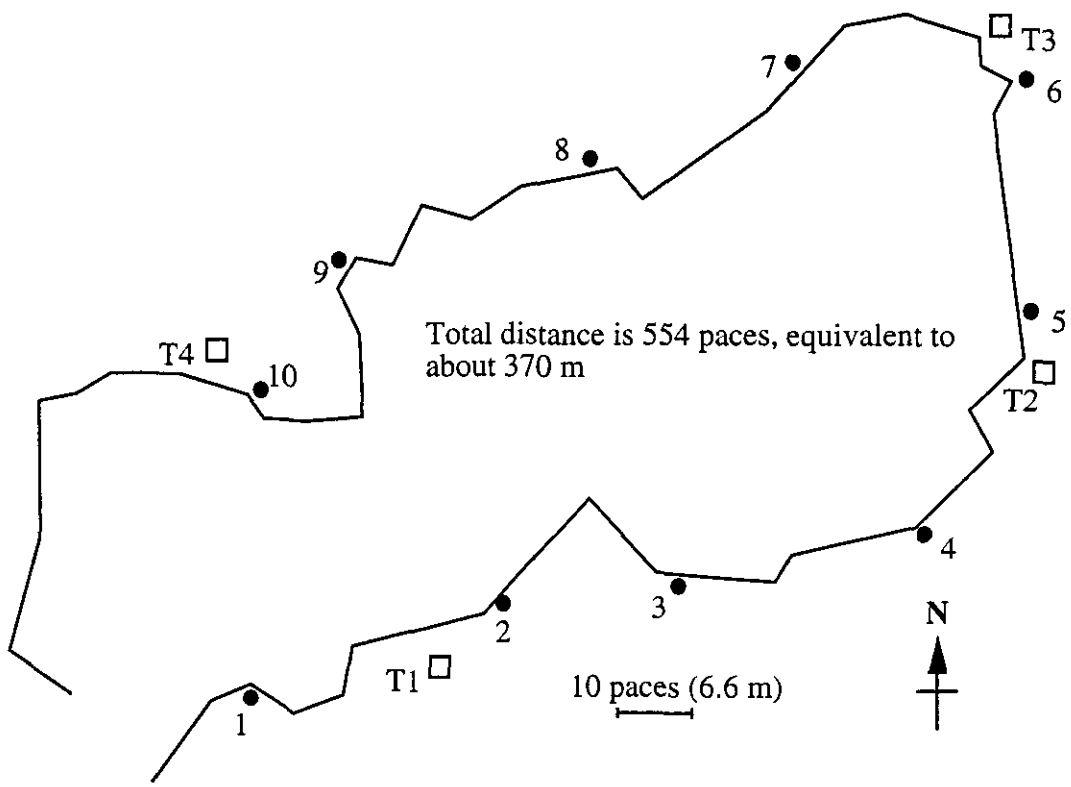
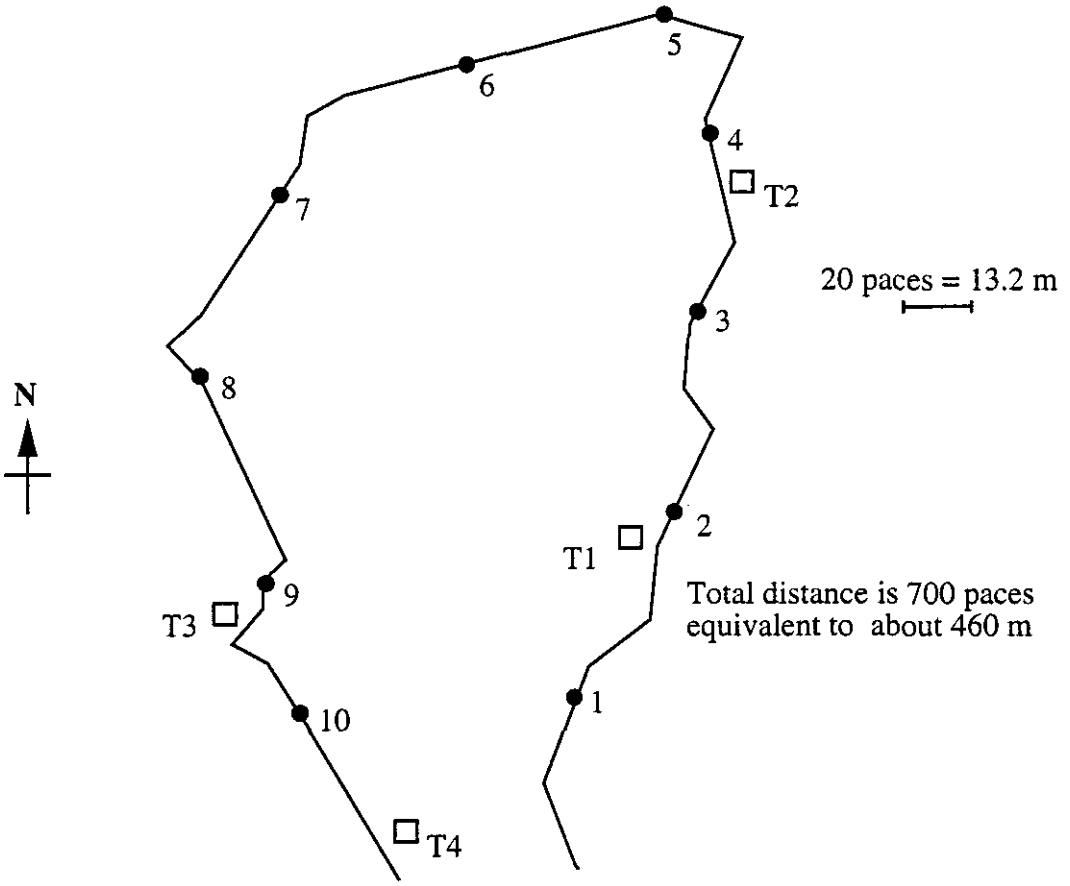


Fig. 3.1. Walk-and-count transect routes in (**a**) disturbed and (**b**) undisturbed semi-evergreen forest carried out in 1994. Solid circles and numbers indicate where vegetation sampling occurred. T1 to T4 indicate the positions of the four fruit traps in each habitat.

a. Disturbed evergreen (Block 4) walk-and-count transect route 1994



b. Undisturbed evergreen (primary) walk-and-count 1994

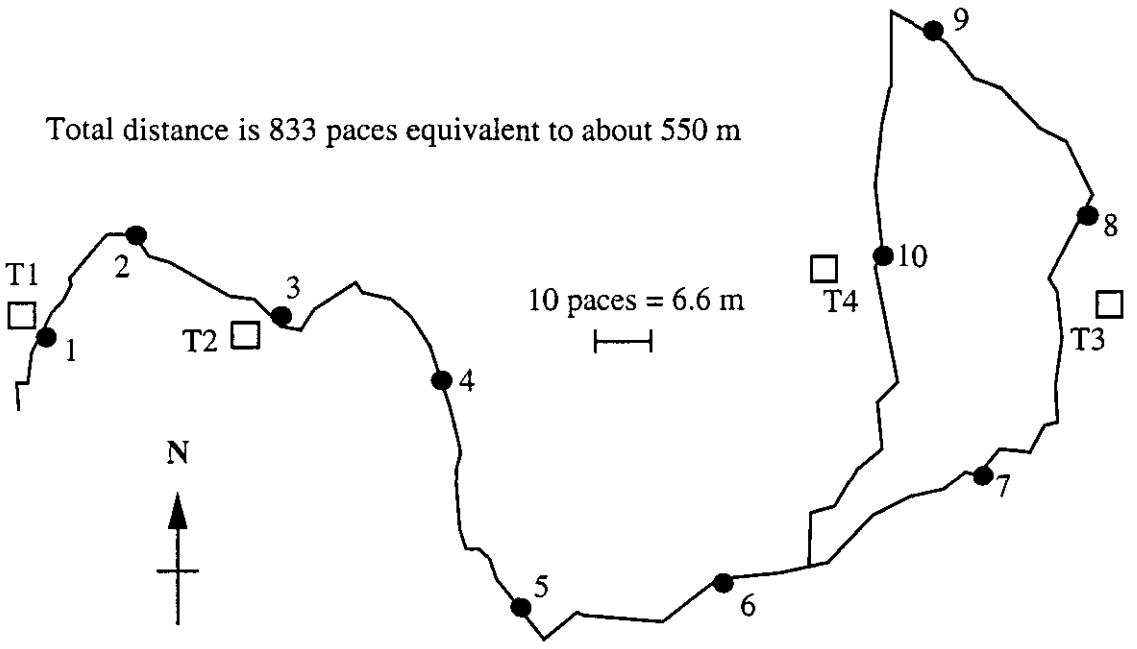


Fig. 3.2. Walk-and-count transect routes in (**a**) disturbed and (**b**) undisturbed evergreen forest carried out in 1994. Solid circles and numbers indicate where vegetation sampling occurred. T1 to T4 indicate the positions of the 4 fruit traps in each habitat.

Over four weeks the disturbed semi-evergreen forest was walked for 1001 person-minutes, undisturbed semi-evergreen for 894 person-minutes, undisturbed evergreen forest for 720 person-minutes and the disturbed evergreen forest for 780 person-minutes. The sampling was carried out each day for four weeks, unless it was raining or it had been raining up to 1 hour previously.

In each of the four habitats there were four locations where both a canopy (minimum of 10 m off the ground) and an understorey trap (1 m off the ground), were placed (Figs. 3.1 and 3.2). The four traps in each habitat were baited, placed in the canopy and then run for four consecutive days. This sampling was repeated for another four days, two weeks later (Table 3.1). The traps were baited at dawn and then inspected in the early morning and late afternoon every day during the trapping period. A preliminary 13 hour fruit trapping survey was carried out hourly in six traps in the undisturbed semi-evergreen habitat to investigate butterfly activity. For species which could be identified in the field, their presence in the traps was recorded and they were marked and released, otherwise they were collected. A canopy photograph was taken and a 10 x 20 m quadrat set up to calculate tree basal area at each of the fruit trap locations along the walk-and-count transect route (Sec. 3.2.4).

The similarity between habitats and sampling methods was determined using the Dice association index M = J / min (A,B), where J is the number of species shared in the comparison and min (A,B) is the total number of species in the smaller of the two being compared (Wolda 1981). Whereas the Sorensen similarity index assumes similar sized samples, the Dice association index takes into account variation in sample size, for example, the fruit trap samples being smaller than the walk-and-count samples. This is because fruit trapping is only dealing with a guild of a maximum of 60 fruit-feeding butterfly species which is a small subset of the much larger pool of butterfly species found in South-East Trinidad forests. The similarity of the butterfly assemblage found in the disturbed versus the undisturbed habitat in each forest type were examined as well as the

similarity found between the disturbed habitats in the two forest types and the undisturbed habitats in the two forest types.

Butterflies were identified following methods described in Ch. 2.

3.2.3. The analysis of species accumulation plots

The number of species encountered after the same sampling effort in each pair of habitats were compared for each forest type. The species accumulation curves for each habitat can be characterised and compared using the power function $S=cE^b$, where S is number of species, E is sampling effort and b and c are coefficients describing the shape and position of the curve.

As the interpretation of shape (and therefore accumulation rate) was sensitive to the total number of species in a habitat, the S axis was scaled to fraction of species accumulated (S'). The function was then linearized by a log-log transformation and $\log_e S'$ regressed against $\log_e E$. This provided estimates of accumulation rate, b (with errors), which characterise the sampling method and habitats and therefore allowed statistical comparison between the disturbed and undisturbed habitats to be made, and also between the two sampling methods in the same habitat.

3.2.4. Measurement of tree basal areas and canopy openness

Tree basal area should be negatively correlated with canopy openness because (a) crown area is usually linearly related to the basal area of a tree (Heinsdijk 1953, Swellengrebel 1959) and (b) canopy openness increases with increased removal of basal area (Steege *et al.* 1994).

Basal area was determined in 10 m x 20 m quadrats at each of 10 points along the butterfly walk-and-count transects in each forest habitat. A girth at breast height (gbh) measurement was taken for each tree > 10 cm gbh, the tree identified, and its co-ordinate recorded. In the centre of each of these quadrats, to determine *relative* openness, photographs of the canopy from 40 cm above ground level were taken using a 35 mm lens. From these photographs, canopy openness values were evaluated using IMAGE, a public domain software package. This program was used to express the light area of the photograph (canopy openness) as a percentage of the total image area.

3.3. Results

3.3.1. Peak activity times for butterfly abundance

A single day 12 hour walk-and-count transect, undertaken every hour in the disturbed semi-evergreen forest habitat, suggested a peak in abundance of the number of species and individuals at 3 pm (Fig. 3.3).

A similar single day survey over 13 hours of six fruit traps in the undisturbed evergreen forest habitat revealed a bimodal peak in distribution of number of species and individuals feeding on fruit (Fig. 3.4). The most individuals were caught between 09:30 and 11:30, the most species at 10:30 am. The number of individuals only dropped slightly before peaking again at 15:30, with the maximum number of species being caught at 14:30.

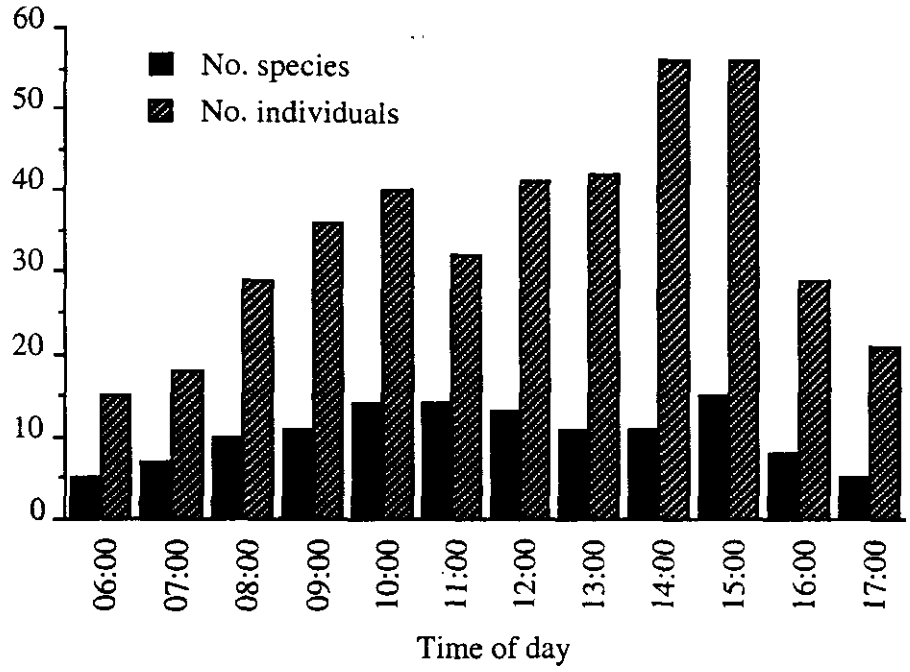


Fig.ure 3.3. Number of butterfly species and individuals encountered each hour over 12 hours of walk-and-count transects in the disturbed semi-evergreen forest (1995).

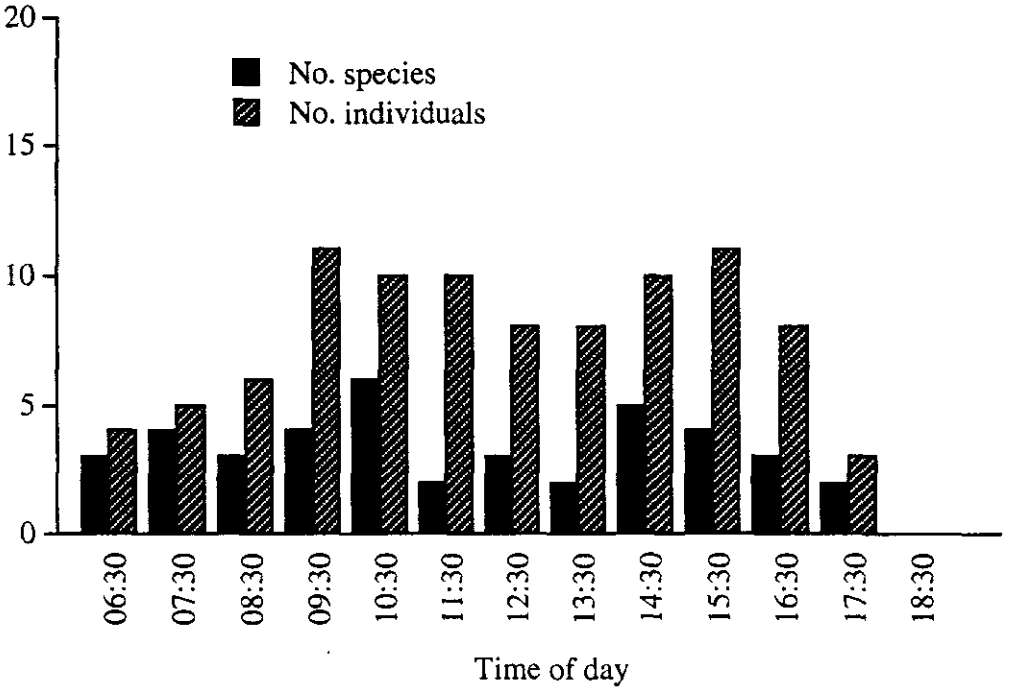


Figure 3.4. Number ofspecies and individuals encountered each hour over 13 hours in six fruit traps (three traps at forest edge and three traps 40 m in) in undisturbed semi-evergreen forest (1995).

3.3.2. Butterfly species richness and habitat similarity

In the walk-and-count transects, the two most disturbed habitats in both forest types studied had the highest species richness values and much higher numbers of individuals (Table 3.2).

Table 3.2. Butterfly species richness and total number of individuals found in the disturbed and undisturbed habitats in both forest types using walk-and-count transects.

HABITAT	SEMI-EVERGREEN		EVERGREEN		Total
	Disturbed	Undisturbed	Disturbed	Undisturbed	
Observed number of species (S)	47	37	40	22	80
Number of individuals (N)	390	184	331	41	946

The species richness values in combined canopy and understorey fruit traps was found to be very similar between disturbed and undisturbed habitats in each forest type (Table 3.3). There were generally less species caught in the canopy in all habitats and considerably fewer individuals. Species richness comparisons alone do not take into account the number of species per individuals sampled. In all cases, species accumulated more rapidly per individual in undisturbed forest but disturbed forest had higher abundance.

Table 3.3. Butterfly species richness and number of individuals caught in fruit traps set in the canopy, understorey and both forest strata together, in the disturbed and undisturbed habitats in both forest types.

	Semi-evergreen						Evergreen					
Habitat	Disturbed			Undisturbed			Disturbed			Undisturbed		
Fruit trap	All	U	C	All	U	C	All	U	C	All	U	C
No. of species	17	17	6	17	13	8	11	9	4	15	10	9
No. individuals	146	133	13	102	86	16	89	66	23	48	34	14

Moderately similar butterfly assemblages were found when comparing the walk-and-count survey data for the disturbed and undisturbed habitats in each forest type (Dice association index values of 0.54 and 0.56, Table 3.4). Greater similarity values were obtained when the butterfly assemblages were compared for the two disturbed habitats in the two different forest types (0.63), and likewise, for the two undisturbed forest habitats (0.65) (Table 3.4).

Table 3.4. Dice association index values of the similarity of butterfly assemblages between disturbed (D) and undisturbed (U) forest habitats in two forest types and between forest types in disturbed and undisturbed habitat. Comparisons are made for species encountered on walk-and-count transects and in understorey, canopy and combined (both understorey and canopy) fruit traps.

	Semi-evergreen	Evergreen		
	D vs U	D vs U	D vs D	U vs U
Walk-and-count transect	0.54	0.56	0.63	0.65
Understorey fruit traps	0.75	0.63	0.77	0.88
Canopy fruit traps	0.67	0.25	0.25	0.43
Combined fruit traps	0.67	0.55	0.64	0.75

Higher association index values were found in the understorey (0.75 and 0.63) than in the canopy fruit traps (0.67 and 0.25) when the butterfly assemblages in the disturbed and undisturbed habitats in each forest type were compared (Table 3.4). Strong similarity in the understorey fruit trap butterfly assemblages was also seen when the butterfly species in the two disturbed habitats (0.77) and the two undisturbed habitats (0.88) were compared. In contrast, the faunas in the canopy fruit traps in the same comparisons were strongly dissimilar (0.25 and 0.43 respectively, Table 3.4).

In every comparison made between the similarity of butterfly assemblages found using walk-and-count and fruit trapping techniques, the greater similarity values were found in the disturbed habitat rather than the undisturbed and in the understorey rather than the canopy (Table 3.5).

Table 3.5. Species similarity between sampling techniques.

Similarity values, using the Dice association index, of species assemblages found between walk-and-count transects and fruit trapping in the understorey, canopy and both (understorey and canopy combined).

	Semi-evergreen		Evergreen	
	Disturbed	Undisturbed	Disturbed	Undisturbed
Understorey	0.75	0.58	1.00	0.38
Canopy	0.50	0.29	0.75	0.13
Combined	0.75	0.47	0.91	0.25

3.3.3. Species accumulation

Species accumulations were plotted for butterfly species encountered in each habitat during four weeks of walk-and-count transects (Fig. 3.5a & b). For the semi-evergreen disturbed and undisturbed habitats the species accumulation plots appeared to be curvilinear and asymptotic, implying that fewer additional species were being encountered (Fig. 3.5a). The undisturbed evergreen plot, however, was linear, and the latter part of the disturbed close to linear, implying that a lot more sampling effort was needed before the total number of species would be encountered (Fig. 3.5b).

When rates of species accumulation (slope of the log fraction of species accumulated against log sampling effort) were compared between habitats for the walk-and-count data (Figs. 3.6a & b), it was found that the habitats were ranked: undisturbed evergreen <

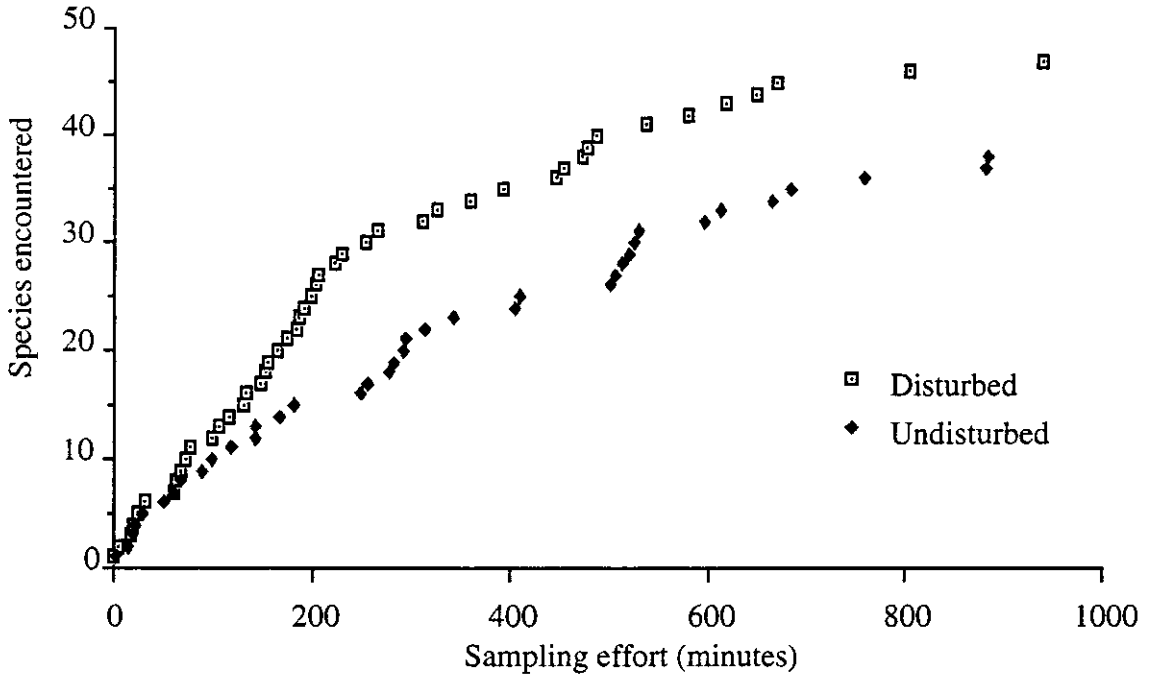
undisturbed semi-evergreen < disturbed semi-evergreen < disturbed evergreen (Table 3.6). The rates of species accumulation for the two undisturbed habitats were not significantly different from one another (F=3.95, p>0.05, df=1,55), but species accumulated significantly slower in the undisturbed evergreen habitat than both the disturbed evergreen habitat (F=6.47, p<0.05, df=1,64) and the disturbed semi-evergreen habitat (F=4.60, p<0.05, df=1,64). There was no significant difference in species accumulation rate between the undisturbed semi-evergreen and either the disturbed semi-evergreen habitat (F=0.027, p>0.05, df=1,81) or the disturbed evergreen habitat (F=0.40, p>0.05, df=1,81), or between the disturbed semi-evergreen and the disturbed evergreen habitat (F=0.23, p>0.05, df=1,90).

Table 3.6. Regression statistics of log-log species-time plots.

Summary of regression statistics for log fraction of species accumulated against log sampling effort for the two sampling methods (F: fruit trap data, W: walk-and-count data).

	Semi-evergreen				Evergreen			
	Disturbed		Undisturbed		Disturbed		Undisturbed	
	F	W	F	W	F	W	F	W
Regression coefficient	0.71	0.65	0.64	0.64	0.35	0.67	0.57	0.54
S.E.	0.09	0.02	0.02	0.01	0.03	0.02	0.04	0.03
r^2	0.91	0.97	0.99	0.99	0.98	0.97	0.97	0.93

a) Semi-evergreen forest



b) Evergreen forest

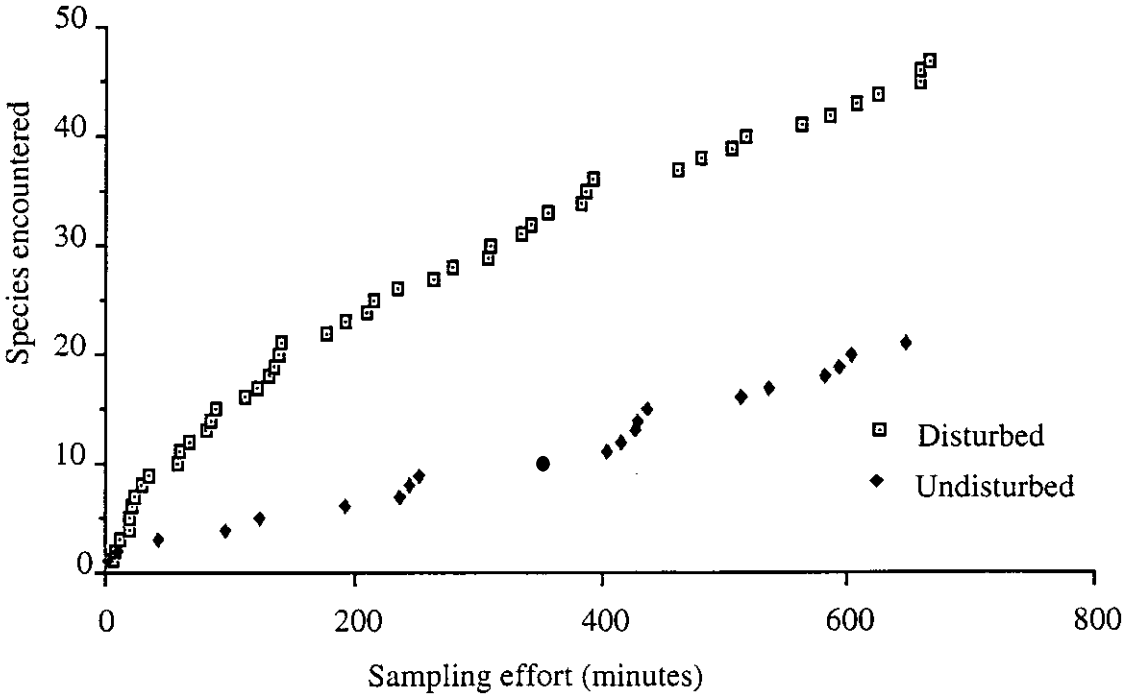
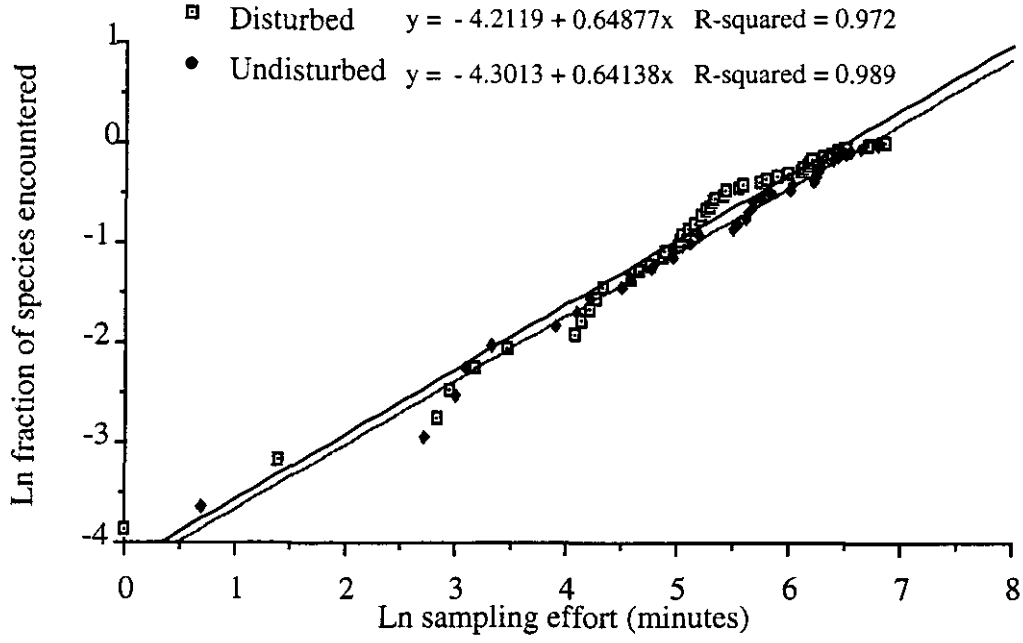


Figure 3.5. Species accumulations for walk-and-count transects in each forest type.

a) Walk-and-count

Semi-evergreen forest



b) Walk-and-count

Evergreen forest

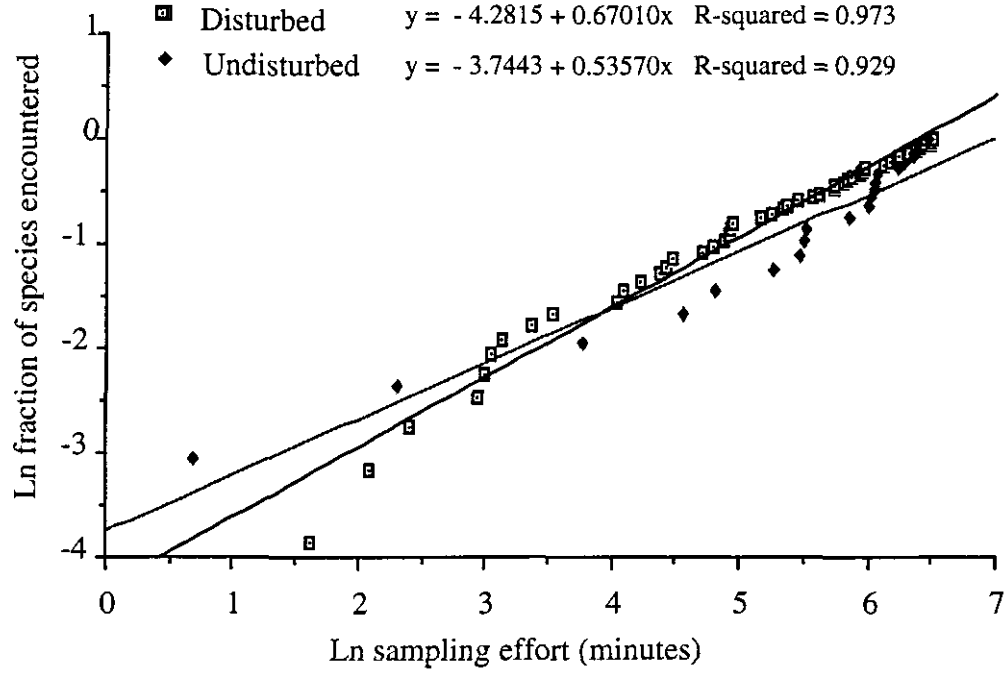


Figure 3.6. Regressions of natural log-log plots of fraction of species encountered against sampling time for walk-and-count transects.

Species accumulation plots were also made from combining the understorey and canopy fruit trap data (Fig. 3.7a & b). Here species richness values after 1728 trap hours were the same for the disturbed and undisturbed habitat in the semi-evergreen forest, both accumulating 17 species. The undisturbed habitat species accumulation curve, however, was more linear than the disturbed habitat. In the evergreen forest, 15 species were encountered in the undisturbed and 11 in the disturbed habitat after 1440 trap hours.

The ranking of the species accumulation rates (Fig. 3.8a & b) for the fruit trap data was found to be: disturbed evergreen < undisturbed evergreen < undisturbed semi-evergreen < disturbed semi-evergreen (Table 3.6). The rate of accumulation of fruit-feeding species in the disturbed evergreen habitat (Fig. 3.8b), found to be the highest with the walk-and-count data, was the lowest with the fruit trap data. Species accumulated at a significantly lower rate in the disturbed evergreen habitat compared to any of the other three habitats (undisturbed evergreen, F=37.93, p<0.001, df=1,22; undisturbed semi-evergreen, F=48.92, p<0.001, df=1,24; disturbed semi-evergreen, F=70.78, p<0.001, df=1,24). The undisturbed evergreen habitat accumulated species significantly slower than the semi-evergreen disturbed habitat (as found with the walk-and-count data, F=13.65, p<0.001, df=1,28) but was not significantly different from the other undisturbed habitat in the semi-evergreen forest (F=3.89, p>0.05, df=1,28).

When species accumulation rates were compared between the two butterfly sampling methods used in each habitat, there was found to be no significant difference for three of the habitats (undisturbed evergreen, F=0.49, p>0.05, df=1,32; undisturbed semi-evergreen, F=0.0006, p>0.05, df=1,51; disturbed semi-evergreen, F=1.17, p>0.05, df=1,60), but a highly significant difference for the disturbed evergreen habitat (F=14.76, p<0.001, df=1,54).

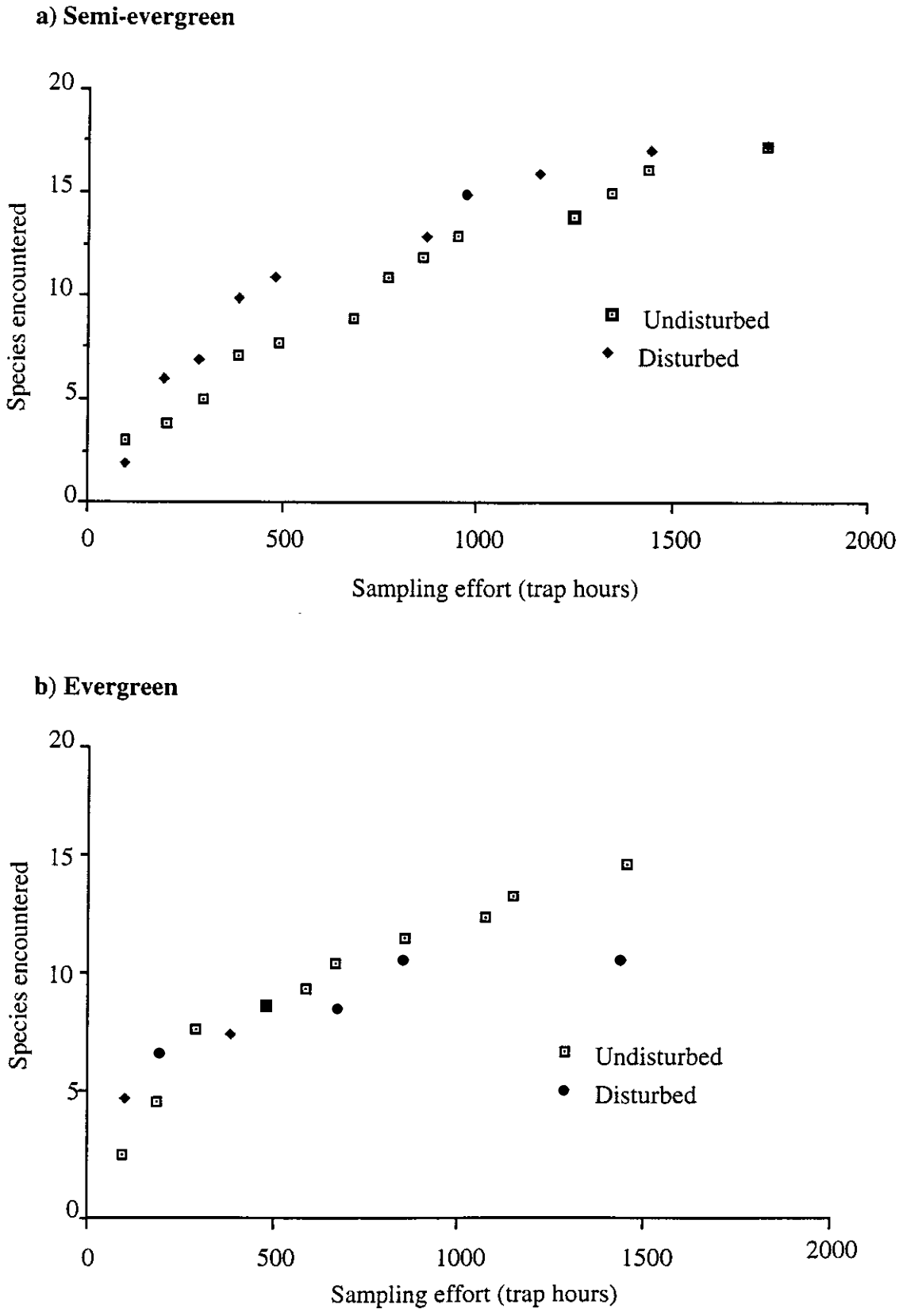
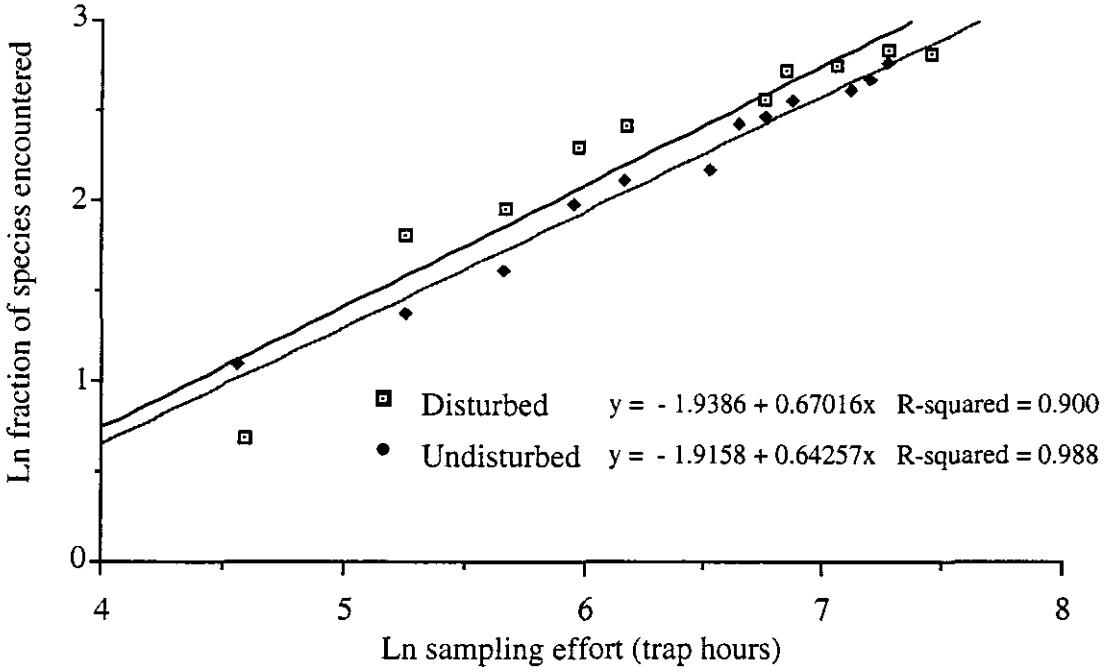


Figure 3.7. Combined species accumulations for fruit-trapping in the understorey and canopy of each forest type.

a) Fruit traps (understorey and canopy combined)

Semi-evergreen forest



b) Fruit trap (understorey and canopy combined)

Evergreen forest

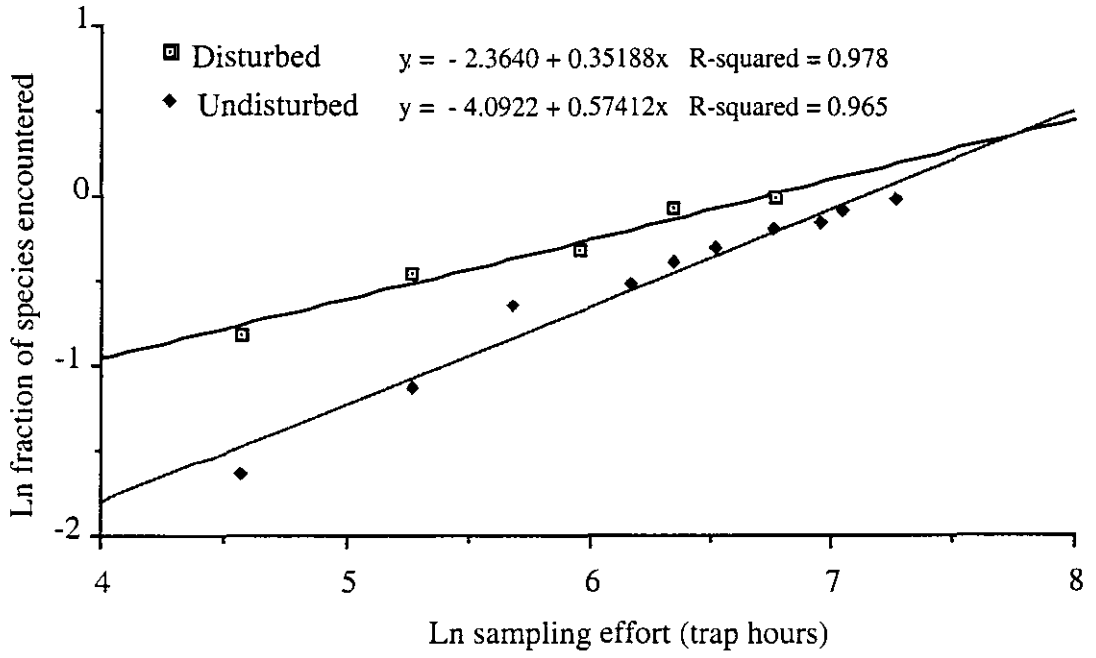


Figure 3.8. Regressions of natural log-log plots of fraction of species encountered against sampling time for combined understorey and canopy fruit traps

3.3.4. Tree basal areas and canopy openness

There was a significant difference between the mean basal areas (Table 3.7; one way ANOVA, F=3.124; df 3, 36; p=0.038). However, there was only a significant difference between the undisturbed evergreen forest mean basal area value and that of the disturbed semi-evergreen forest, which was approximately half the undisturbed evergreen forest basal area (Tukey T-Method test (Sokal and Rohlf 1981), MSD=26.65; p<0.05). The disturbed and undisturbed semi-evergreen and disturbed evergreen forests were not significantly different in basal area. The basal area of the undisturbed evergreen forest in Trinidad was very similar to that found in lowland Jamaican primary forest (Table 3.7).

Table 3.7. Tree basal areas and canopy openness values.

Comparison of tree basal areas for four different forest habitats in Trinidad and for a tropical lowland forest below 600 m in Jamaica (Tanner, E.V.J., A.M. Sugden and V. Kapos In: Swaine *et al* 1987).

Forest habitat	Min. gbh (cm)	Basal area (m^2 ha^{-1})	S.E.	Mean canopy openness (%)	S.d.
Evergreen undisturbed forest	10	62.95	0.692	11.0	1.08
Evergreen disturbed	10	38.05	0.374	12.3	6.99
Semi-evergreen undisturbed	10	37.00	0.383	4.94	2.66
Semi-evergreen disturbed	10	33.20	0.426	7.61	6.75
Primary forest (Jamaica)	10	65.40	-	-	-

Mean canopy openness values were obtained (Table 3.7) which were not significantly correlated with tree basal areas for either the disturbed semi-evergreen habitat (r=0.549; df=8; p>0.05), the undisturbed evergreen forest habitat (r=0.144; df=8; p>0.05) or for both habitats (r=0.238; df=16; p>0.05). Although mean canopy openness values for these two habitats with the greatest difference in mean basal area were fairly similar, the variance

(s^2) in canopy openness values was much greater for the disturbed semi-evergreen habitat than the undisturbed evergreen forest (disturbed semi-evergreen mean openness = 7.61; n=10; s^2=45.6 and undisturbed evergreen forest mean openess = 11.0; n=10; s^2=1.17).

3.4. Discussion

A 12 hour walk-and-count survey revealed a peak in the number of species and number of individuals at 3 pm (Fig. 3.2.a). Sampling at these times of peak species number and abundance would, therefore, be most efficient and productive, if the aim of the sampling was to encounter the majority of the butterfly assemblage. This peak in number of species and number of individuals at 3 pm may have proved more conclusive with replication in this habitat and others, and is a recommended preliminary measure prior to sampling, time permitting. Due to time constraints, replication was not possible in this study. It is unlikely, however, that these times of peak species number and number of individuals recorded, will coincide with the peak in activity of all species. The Brassolinae *Caligo* species, for example, although seen throughout the day, are crepuscular in courtship. The two *Dynastor* species (Brassolinae) found in Trinidad, *D. darius darius* and *D. macrosiris,* are entirely crepuscular. So much so, that the only three specimens of *D. macrosiris* in the Barcant collection captured between 1931 and 1962, were two which flew into houses at dusk and one which flew into a car, also at dusk (Barcant 1970). Only one unconfirmed sighting of *D. darius darius* hovering around a fruit trap at dusk in the disturbed semi-evergreen habitat was made in the course of field work for this thesis.

A similar 13 hour fruit trapping survey of 6 traps revealed a peak in the number of individuals at 9:30 and 15:30, and in number of species at 10:30 and 14:30 (Fig. 3.2.b). Sampling at these times and after, assuming individuals could not escape from the traps, is less important than for walk-and-count sampling, as trapping is cumulative between sampling times, assuming individuals do not escape once trapped.

The walk-and-count census carried out in South-East Trinidad revealed that butterfly species richness was greater in the disturbed forest habitats. Species accumulation

functions (Fig. 3.3) clearly show this disparity in species richness in habitats, the more disturbed habitats in both forest types having 21 % and 110 % more species than the undisturbed habitats over the same sampling period. In Costa Rica, a road transect, following a wide, continuous light-gap, produced 74 % more butterfly species than a trail transect that traversed undisturbed forest with scattered light gaps (Sparrow 1994). Work in forest fragments in Manaus, Brazil, also showed a dramatic increase in butterfly species richness in forest habitats with increased light levels in the understorey, such as in large internal clearings and fragments which were semi-isolated (increased proportion of edge habitat), compared with inside forest (Brown 1991, Lovejoy *et al.* 1986). These results have parallels in temperate forest habitats where the management of forest and rides to provide a large range of shade levels, has been found to increase the number of habitats suitable to different butterfly species (Warren 1985). In contrast to these results, work carried out in Malaysia found both butterfly species richness and diversity to be higher in unlogged than in logged forests (Hill *et al.* 1995).

It is likely that habitats with slower rates of species accumulation may indicate a butterfly assemblage with a greater evenness in abundance distribution between species because new species are accumulated at a low but steady rate. Conversely, higher rates of species accumulation may indicate a butterfly assemblage composed of abundant species (encountered with little sampling effort) and rare species encountered infrequently after much greater sampling effort. On the other hand, it may be that there is no difference in distribution (evenness) but one butterfly assemblage is more abundant than the other.

Comparison of walk-and-count species accumulation rates between habitats revealed that the undisturbed evergreen habitat was significantly lower than the two disturbed habitats, but not significantly different from the other undisturbed habitat (Table 3.6). Thus the apparent lower species richness in undisturbed forest may be due to the short sampling effort. A similar result was found by workers looking at the rates of species accumulation

of birds in Costa Rican lowland forest habitats at La Selva Biological Station. Species accumulation curves based on the first 1000 captures revealed that rates of species accumulation (the slopes of the species accumulation curves) were significantly higher in young secondary growth forest than in old secondary growth forest and significantly higher in the old secondary growth forest than in primary forest (Blake *et al.* 1990).

Comparisons of fruit trap species accumulation rates also found no significant difference between the undisturbed habitats, with significantly slower rates of species accumulation than found in the disturbed semi-evergreen forest. However, in stark contrast to the walk-and-count data which showed the highest species accumulation rate in the disturbed evergreen forest habitat, fruit trap data revealed this same habitat had a significantly lower species accumulation rate compared with all other habitats. From the species accumulation curves (Fig. 3.7) it can be seen that five of the 11 species encountered through fruit trapping in the disturbed evergreen habitat were encountered in the first 96 trap-hours of trapping. The next 1344 trap-hours added only six more species to the list. Through walk-and-count sampling, new species were continually encountered over the sampling period in the disturbed evergreen habitat. By also using an alternative sampling method, fruit trapping, a completely different picture of species accumulation was unveiled. Only through the concurrent use of these two sampling methods was this difference between butterfly assemblages within the same habitat detected. Furthermore, the importance of using measures of accumulation rate to describe a habitat's butterfly fauna, which take into account sampling effort, compared with species counts, is clear, as very different interpretations of forest disturbance may result. Interpretation of these results could be affected by the detectability of butterflies on walk-and-count transects which may have been lower in the darker understorey of the undisturbed forest habitats than in the disturbed habitats. However, the differences in visibility between the undisturbed and disturbed habitats were small and unlikely to have led to significant differences in species detection rates.

The species richness of the butterflies in the canopy is only known from a few examples involving fruit trapping (DeVries 1988) or direct observation (Hill 1992, Jackson 1961). It is the general impression of DeVries that any Costa Rican forest habitat below 1900 m has a higher butterfly diversity in the canopy than in the understorey, although he admits more work is needed (DeVries 1987). Disturbance can disrupt this stratification between the canopy and understorey faunas. DeVries has stated that 'butterflies treat disturbances as if the canopy had come to the ground' (DeVries 1987) and 'if differences in light levels are important for maintaining stratification in rainforest buterflies, we might predict that in habitats without pronounced differences in light levels (ie., disturbed forest, in deciduous forest in the dry season, or along forest edge), stratification will not be as distinct as in closed canopy forest' (DeVries 1988). This was highlighted in the present study when the butterfly faunas sampled by walk-and-count transects were compared to those caught in the canopy fruit traps. High dissimilarity was evident in the two undisturbed habitats sampled (mean Dice association index value of 0.21) whereas similarity was much greater in the disturbed habitats (mean association index value of 0.61). This suggests that the canopy of the disturbed forest habitats are too disturbed to maintain a distinct canopy fauna from an understorey one, but the undisturbed habitats do have a stratified butterfly assemblage.

The butterfly assemblages encountered through walk-and-count surveys in the same disturbance level (ie. both disturbed or both undisturbed habitats in different forest types) showed greater similarity than between the disturbed and undisturbed habitat in the same forest type (Table 3.4). This implies that within a region of forest, butterflies are characteristic of disturbance rather than forest vegetation type. This lends further weight to the belief that butterfly faunas can be used as bioindicators of disturbance. For the fruit trapped butterflies, the understorey butterfly assemblages were more similar than the canopy butterfly assemblages between the disturbed and undisturbed habitats in the same forest type, and in different forest types within the same disturbance category (Table 3.4).

Fruit trap studies are by design only sampling the relatively small guild of fruit-feeding butterflies, approximately 60 species for Trinidad (Barcant 1970). This would suggest that the number of species encountered when fruit trapping would be less than the number encountered on walk-and-count transects, which was indeed the case. Furthermore, despite 1500 fruit trap hours of sampling, it is likely that the species accumulation plots were far from capturing the total number of species in each habitat. This was shown to be the case when the data for the 864 trap hours (4 traps) of fruit trapping in the understorey of the undisturbed semi-evergreen forest in 1994 was compared with the data from over 10,000 trap hours (18 traps) in 1995 (data from the study in Ch.4) at the same site (Fig. 3.9), revealing a striking similarity in species accumulation between years at the same forest site, despite the use of a different numbers of traps (proof in the concept of trap hours) and despite different trap layouts (proof in the robustness of trapping data to describe a habitat between years).

Despite the difference in total number of species, of the 13 species encountered in 1994, seven were in the top 10 most abundant species for 1995. Hence the fruit trapping in the 1994 study (Chapter 3) and the comparisons made between habitats, were likely to have been amongst the most abundant species of each habitat. This fact, combined with the use of accumulation functions (which were all based on highly significant overall fits to the data), suggest that relatively short sampling periods can provide valuable insights into the response of the core of the butterfly assemblage to disturbance.

Whilst the importance of undisturbed habitats for certain butterfly species is clear, this work has shown that disturbed forest habitats also have a part to play, providing a rich mosaic of microhabitats varying in light and abiotic conditions, attracting secondary-growth, light-loving butterflies from the forest edge (Brown 1991, DeVries 1988, Hill *et al.* 1995, Lovejoy *et al.* 1986, Sparrow 1994).

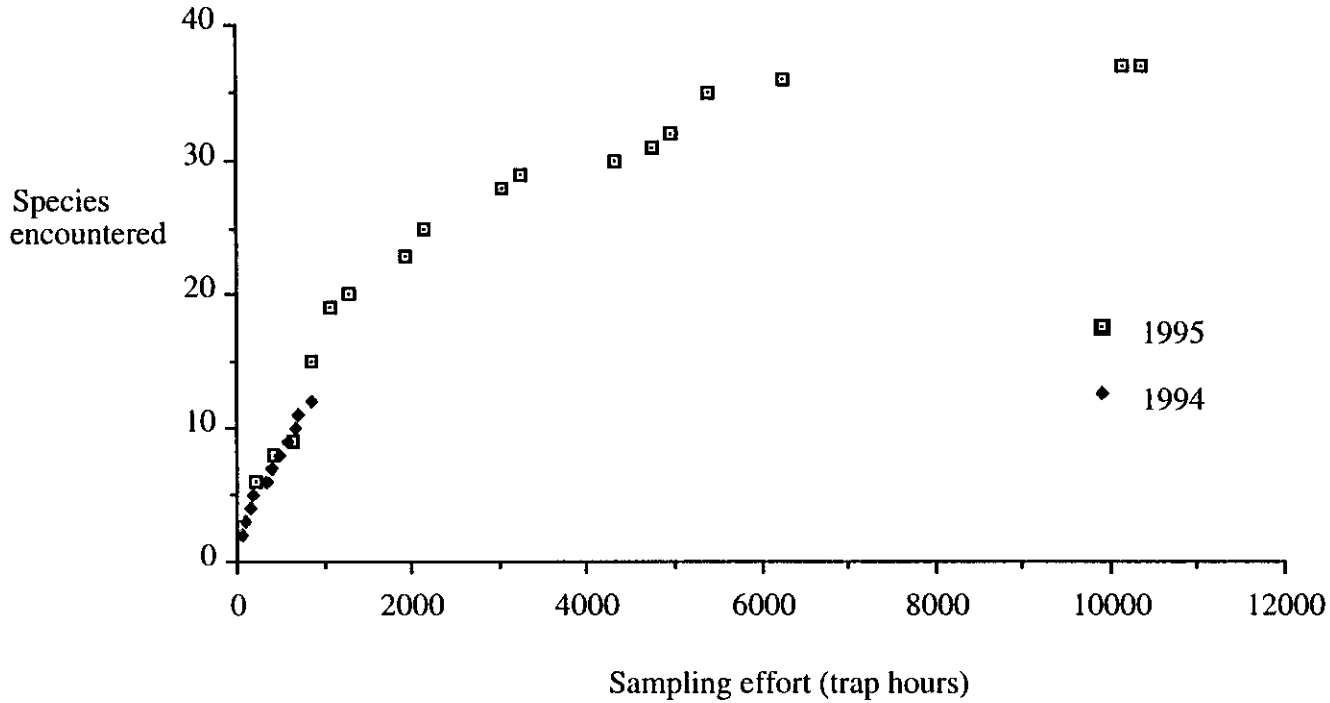


Figure 3.9. Fruit trap species accumulations in the understorey of undisturbed semi-evergreen forest for 1994 (4 traps) and 1995 (18 traps).

Chapter 4

Butterfly movement patterns within and between forest blocks

4.1. Introduction

Having looked at general trends of butterfly species richness and comparing species accumulation rates and similarity between disturbed and undisturbed forest habitats (Ch.3), the focus of study was reduced further. This was achieved by (a) investigating individuals from just the fruit-feeding guild of butterfly species, and their movement patterns, and (b) concentrating on one habitat, the undisturbed semi-evergreen habitat, and more specifically, one element of disturbance within that habitat; namely breaks in the forest created by a road and gas-line (Fig. 4.1) and the effect of a forest edge.

The spatial dynamics of forest butterflies within tropical forests is poorly understood. Vertical stratification has been reported in the fruit feeding butterfly guild (DeVries 1988) and Trinidad (Results and Discussion in Ch.3). The horizontal spatial dynamics of most tropical forest butterfly species remain unknown. Extensive research on species in the Heliconiinae sub-family over the last few decades (Benson 1991, Boggs *et al.* 1981, Cook *et al.* 1976, Deinert *et al.* 1994, Ehrlich and Gilbert 1973, Gilbert 1972, Mallet 1986, Menna-Barreto and Araujo 1985, Murawski and Gilbert 1986, Smiley 1978, Swihart 1971, Turner 1971) have revealed several species exhibiting home-range behaviour, remaining resident in an area for the duration of their life, a period of several months in some cases, following learnt daily routes to visit the same nectar and pollen sources before returning to the same communal roosting site each night. Home-range behaviour has also been found in a confined population of *Morpho peleides* in a pocket of Costa Rican forest in the dry season (Young and Thomason 1974).

As fragmentation increases in a landscape, the proportion of edge habitat relative to interior habitat increases. A habitat edge can be extremely significant for small animals such as insects due to abrupt changes in for example light, substrate,water conditions and species composition (Wilcove *et al.* 1986). Species distributions have been affected by alterations in foodplant distribution in edge habitat (Warren 1987a, Warren 1987b) and flight paths have also been reported to have been modified (Wood and Samways 1991). The edge effect of a patch of tropical pine trees on grasshopper abundance in a grassland area was found to be 30 m (Samways and Moore 1991) and workers on the Biological Dynamics of Forest Fragments Project near Manaus, Brazil, reported that most new records of species were from 100 m of the edge, some at 200 m and occasionally, especially on ridges and small clearings, at 300 m (Brown 1991, Lovejoy *et al.* 1984). The distribution of species in a species assemblage, within a habitat, relative to the edge of that habitat, is therefore fundamental if predictions of the effects of increased fragmentation on that species assemblage are to be made. "Much more research is required on edge effects in tropical and subtropical countries" (Samways 1994).

Another major effect of forest fragmentation is the reduced connectivity between patches. Patches will be more or less isolated for a species, depending upon whether the open ground between patches is a barrier to dispersal for that species (Ford 1971). Theoretically, the wider the gap between patches and the more dependent a species is on closed forest, the greater the likelihood of species losses in isolated fragments not being reversed by immigration. It is possible that certain species preferentially move in the central interior environment whilst others move mainly along habitat edges. The presence of breaks of open areas between forest patches may act as a barrier to movements between patches by forest-interior species, reducing mobility, increasing isolation and splitting gene pools. Field observations on birds support the hypothesis that some forest species avoid crossing open areas (Martin and Karr 1986, Opdam *et al.* 1985, van Dorp and Opdam 1987, Willis 1974, Yahner 1983), and the same has been found for forest-dwelling mice (*Apodemus flavicollis*) and carabid beetles (Mader

1984). It has been found that adults of the Adonis blue butterfly *Lysandra bellargus* readily flew 250 m over open calcareous grassland, but appeared not to do so over 100 m gaps of agriculturally improved grass, hedge and scrub (Thomas 1983). Similarly, Warren (1987a,b) found that the heath fritillary *Mellicta athalia* moved along woodland rides between clearings within continuous patches of woodland, but almost never across even short stretches of farmland from one isolated wood patch to another. The lack of empirical studies on movement patterns in insects has been highlighted for all habitats (Collins and Thomas 1991).

In the present study, the movement patterns of different fruit-feeding butterfly species were compared and stratification to a forest edge investigated. Relative dispersal across thin breaks of open ground between large tracts of forest were also investigated. An inability to cross such thin breaks of open ground would have enormous ramifications for species survival in an ever-increasing fragmentation of forest habitats.

The main objectives of the work in this Chapter were:

1) to investigate the distribution patterns of fruit-feeding butterfly species from a forest edge up to 40 m into the forest.

2) to carry out a pilot study to investigate butterfly distribution and movements further into the forest (up to 360 m) from the forest edge.

3) to investigate the effect of thin breaks of open ground between blocks of forest on the movements of fruit-feeding butterfly species.

4.2. Methods

This study was carried out in the Trinity Hills Wildlife Sanctuary in southern Trinidad (Ch. 2) from May 30th to August 26th 1995. The Sanctuary is bisected by a road running parallel to the south coast from Guayaguayare in the South East to Moruga in the South West (Plate 4.1a). This road and a parallel gas-line were used to study the patterns of fruit-feeding butterfly movements both within forest up to the road, and between forest blocks separated by the road and gas-line (Plate 4.1b).

4.2.1. Study 1: forest edge to 40 m into forest

Fruit-feeding butterflies were investigated by trapping in fruit traps (Ch.2). Individual butterflies were identified by uniquely marking each individual (Ch.2), enabling individuals to be followed through space and time. A study site was selected along the Guayaguayare to Moruga road, 150 m from the start of the Sanctuary. A set of three fruit traps were placed at the forest edge, spaced 30 m apart. A set of three were then placed parallel to these, 20 m into the forest, and a further three placed 40 m into the forest. A similar grid of nine fruit traps was set up 500 m further west along the road (Fig 4.1). This study, from May 30th to June 30th 1995, covered 24 days of trapping.

For each species, the proportion of new captures caught in each of the three sets of three traps (at the forest edge, 20 m and 40 m in) were compared, using a G-test, with a 1:1:1 ratio, the proportions expected of an even distribution of individuals between successive sets of traps. This was repeated for the proportion of recaptures of individuals for each species. The distinction is made here between "recapture events" and "recaptures". If an individual was recaptured three times during the study, this was recorded as three 'recapture events' and as one 'recapture'. The numbers of captures and recaptures between each of the three sets of three traps running perpendicular to the forest edge, were tested for significance in the same way. Movements between the two grids of traps 500 m apart were also reported.

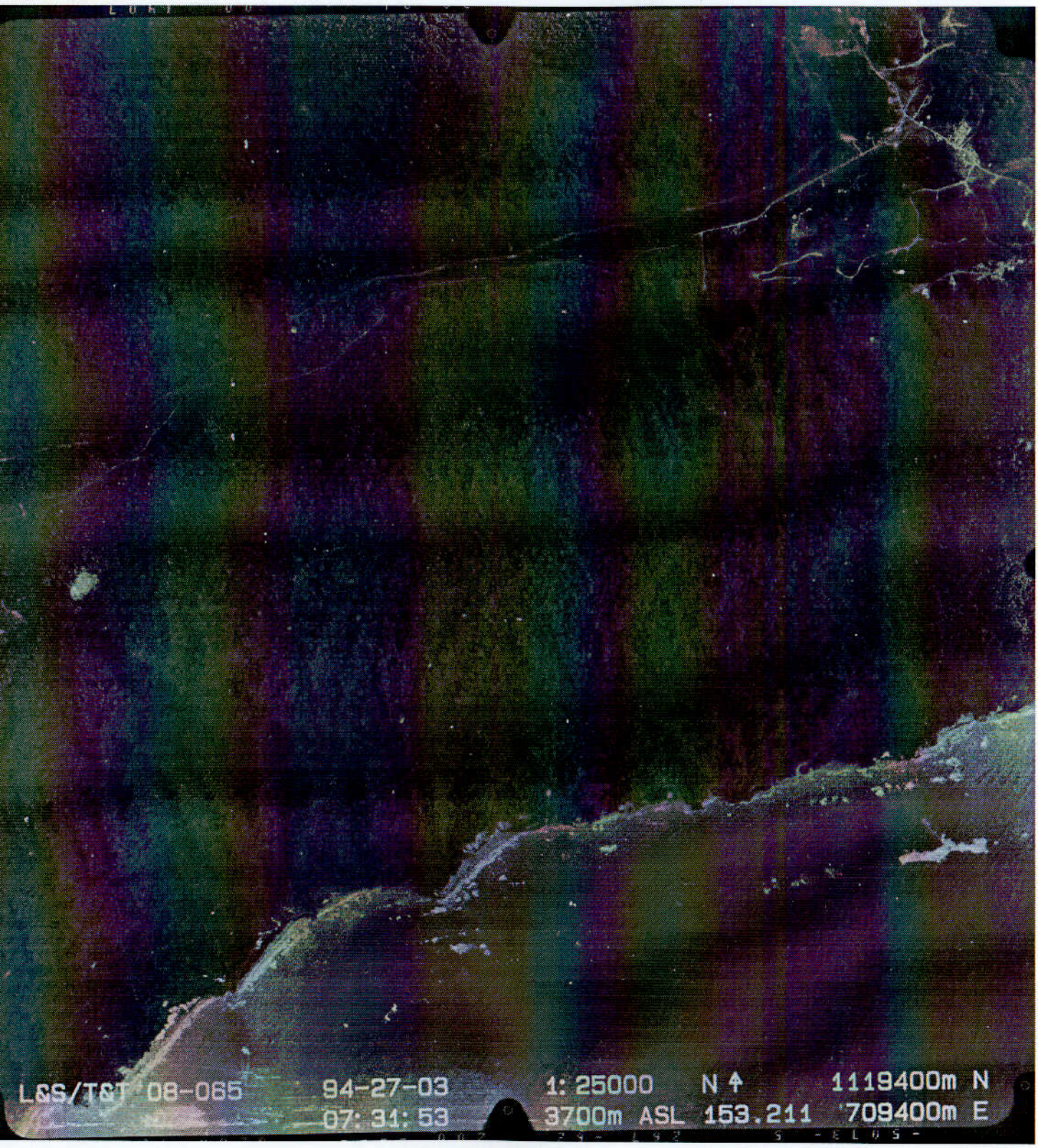


Plate 4.1a. Aerial photograph of the Trinity Hills forest showing the road and gas-line breaks in study 2

Plate 4.1b. The forest breaks, road (top) and gas-line (bottom), used in study 2 to investigate the effect of such forest fragmentation on butterfly movements

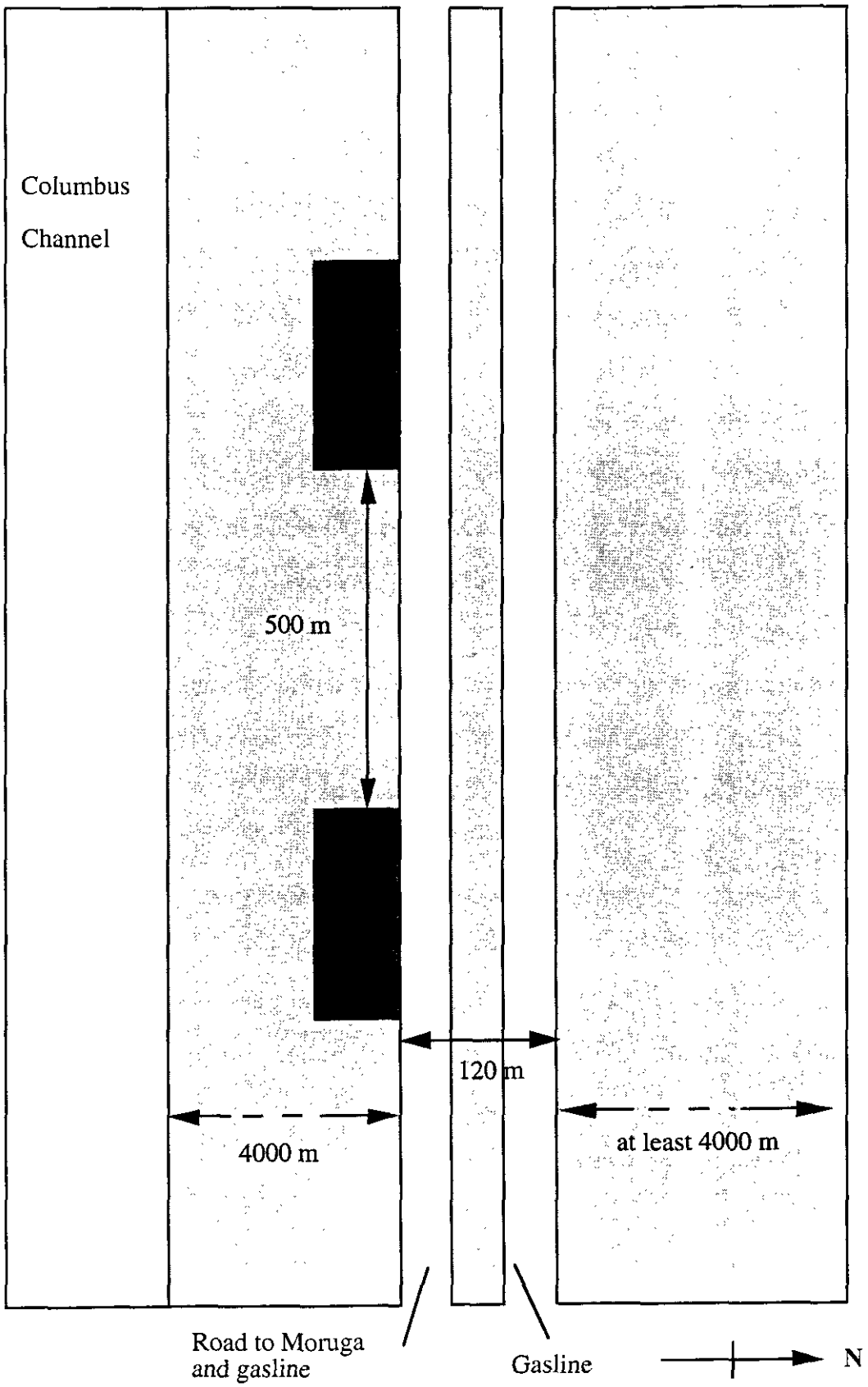


Figure 4.1. The layout of the fruit traps in study 1: from a forest edge to 40 m into forest.

4.2.2. Study 2: movement across breaks in the forest

In order to investigate the movement of butterflies between blocks of forest across breaks, 18 fruit traps were placed in sets of three as illustrated in Fig. 4.2. Three traps were set up 40 m into the forest, parallel to the road, spaced 30 m apart, in the same positions used in study 1 (Sec. 4.2.1). Three further traps were placed due north of these, along the forest edge to the south of the road (again in the same positions as study 1). Three traps were placed north of these, across the break in the forest made by the road (approximately 40 m away) again at the forest edge. The next three were placed 40 m north of these on the north-facing edge, three more about 40 m away across another break in the forest made by a gas-line, along a south-facing edge and three more 40 m into the forest. This study was carried out between the 4th of July and 10th of August 1995 and produced a total of 23 trapping days.

The distribution of new captures of all species was investigated with respect to aspect, so that north and south-facing edges of the strip forest were compared, as were the north and south-facing edges of the large forest blocks.

The overall pattern of recapture events of all species were mapped to examine net movement within and between forest blocks. To investigate relative residency within each of the three forest blocks, the number of recapture events that occurred within each forest block were presented as a proportion of the total number of recapture events that occurred within, into and out of each forest block. The proportions obtained for each block were compared using the G-test.

For the five most abundant species (genus in the case of the *Caligo* species) in terms of number of marked individuals (Appendix B.1), total movements (recapture events) were drawn with respect to each of the six forest strata in the study. This provided a visual description of movement patterns, so that preferred movement patterns within particular forest strata or across particular breaks in the forest could readily be identified.

The recapture data were then used to assess which species had crossed either of the breaks between forest blocks, and if they had crossed, what proportion of the recaptured individuals of that species had done so.

An approach outlined in Munguira & Thomas (1992) to investigate butterfly dispersal across roads in the U.K., was then used to determine whether the road or gas-line had been a barrier to dispersal, for all those species for which sufficient recapture data existed (>5 individuals expected). Capture data from the six traps in the southern forest block and the six traps in the strip forest were used to investigate dispersal across the road, and captures from the six traps in the northern block and the six traps in the strip forest to investigate dispersal across the gas-line. The number of adults recaptured on the opposite side of the road or gas-line was compared with the frequency of recaptures predicted if the road or gas-line was no barrier, using the following calculation from Munguira & Thomas (1992): if p is the proportion of total site captures made on one side of the road and q the proportion on the other, then $2pq$ is the probability of crossing if the road had no effect on movement. Multiplying by the total number of movements recorded (= number of recaptures) gives the expected frequency of crossings. This was then compared with the observed figures using the G-test.

The same method was used to examine the movements between consecutive sets of three traps spaced approximately 40 m apart. This included movements across the road and gas-line (using data from 3 traps either side of the break) but also included movements within each of the large forest blocks and the forest strip. This approach was only possible for a few species with sufficient recapture data (those species with any recaptures between these traps and only those with >5 individuals in expected number of individuals category were tested for significance using the G-test).

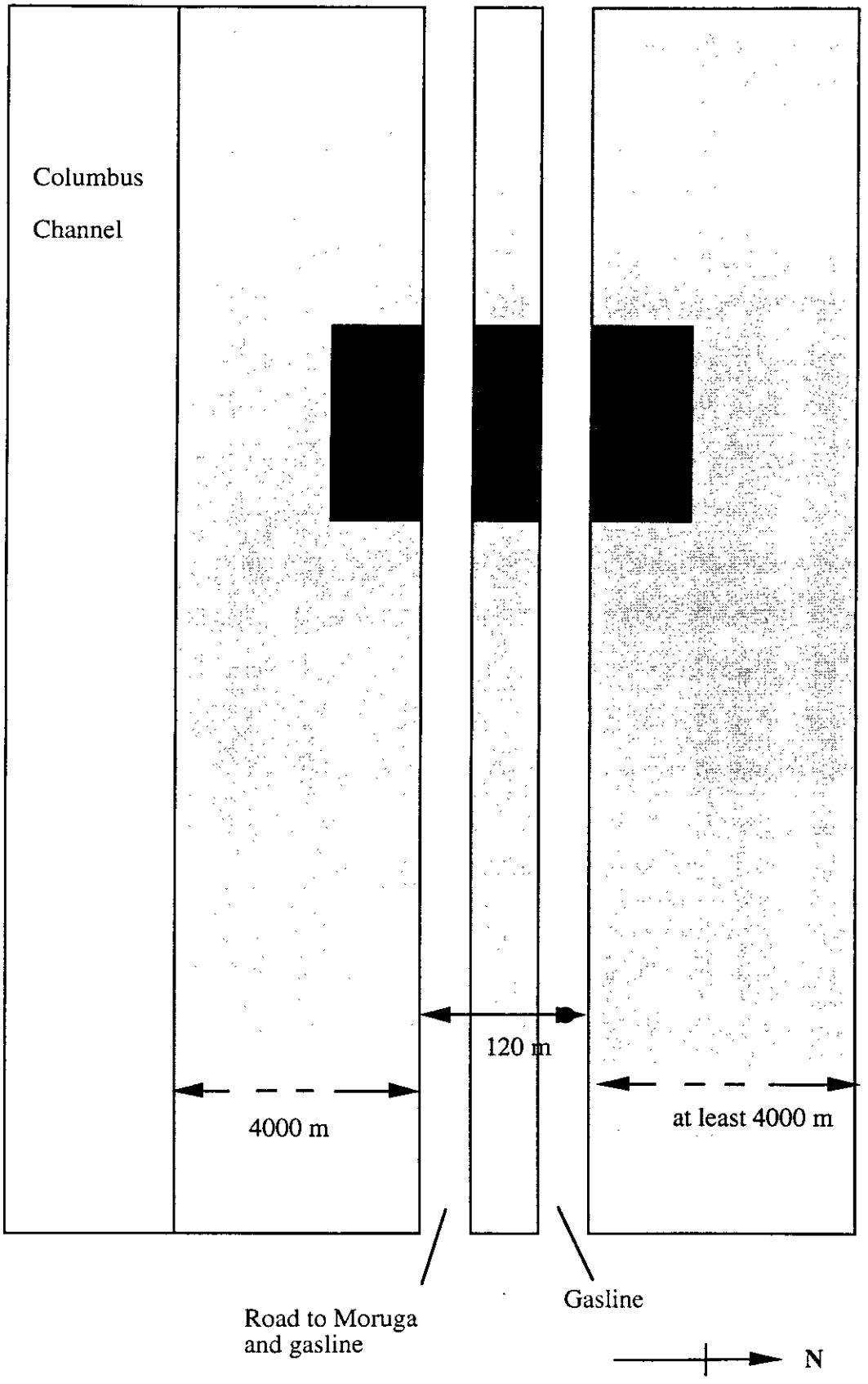


Figure 4.2. The layout of the fruit traps in study 2: movement across breaks in the forest.

From the trapping design in study 2 (Fig. 4.2), it can be seen that there are 18 possible distances that could be flown between successive captures of individuals, from 0 to 209 m. The relative frequency of recapture events recorded over these different distances were calculated and plotted for each species. The relative frequency distributions of distances flown by *Morpho peleides* and *Cissia penelope* were compared and tested for significance using the Kolmogorov-Smirnov Test for Goodness of Fit (Sokal and Rohlf 1981).

4.2.3. Study 3: movements deeper into the forest

Two fruit traps were placed at the forest edge, 30 m apart, at the fruit trap positions used in site 2 (Fig. 4.2), following the completion of study 2. A series of pairs of traps were then placed at 40 m intervals beyond these original two, heading in a southerly direction, perpendicular to the road, into the forest to a distance of 360 m. This was a preliminary investigation, carried out for 7 days between 14th August 1995 and 26th August 1995, with no replication.

Frequency histograms of the new captures caught at each distance were plotted to look at patterns of distribution between different species. Individual movements between traps at different distances into the forest were displayed as arrows on the frequency histograms.

4.3. Results

4.3.1. Study 1: forest edge to 40 m into forest

Over this four week period (24 days trapping), 37 species were encountered (Appendix B.1). Of these, 27 were represented by more than one individual and 23 were recaptured. 581 individuals were marked (new captures) of which 181 were recaptured (31.2 %). There were 354 recapture events recorded overall.

There was no significant difference in number of recapture events at each site (Fig. 4.3), with 161 recapture events recorded in site 1 and 137 in site 2 ($G = 1.94$, $p>0.05$, $df=1$). Of species with sufficient captures to merit significance testing, only *Pierella hyalinus* showed a significant inter-site difference, although captures were low, with 10 captures in site 1 and two captures in site 2 ($G= 5.82$, $p<0.05$, $df=1$). *Cissia penelope* was abundant at both site 1 (121 marked individuals, 53 recapture events) and site 2 (115 marked individuals, 45 recapture events), and these differences were not significant ($G = 0.15$, $p>0.05$, $df=1$ for new captures and $G = 0.65$, $p>0.05$, $df=1$ for recapture events). The same was true for new captures of *Morpho peleides* ($G=1.38$, $p>0.05$, $df=1$), *Colobura dirce* ($G=2.69$, $p>0.05$, $df=1$), *Caligo teucer* ($G=1.01$, $p>0.05$, $df=1$), *Cissia hermes* ($G=2.1$, $p>0.05$, $df=1$) and *Taygetis andromeda* ($G=0.44$, $p>0.05$, $df=1$). The similarity of the butterfly assemblages found in the two sites allowed either site to be chosen for study 2. Site 2 was chosen as it was further from the oil compound and habitation.

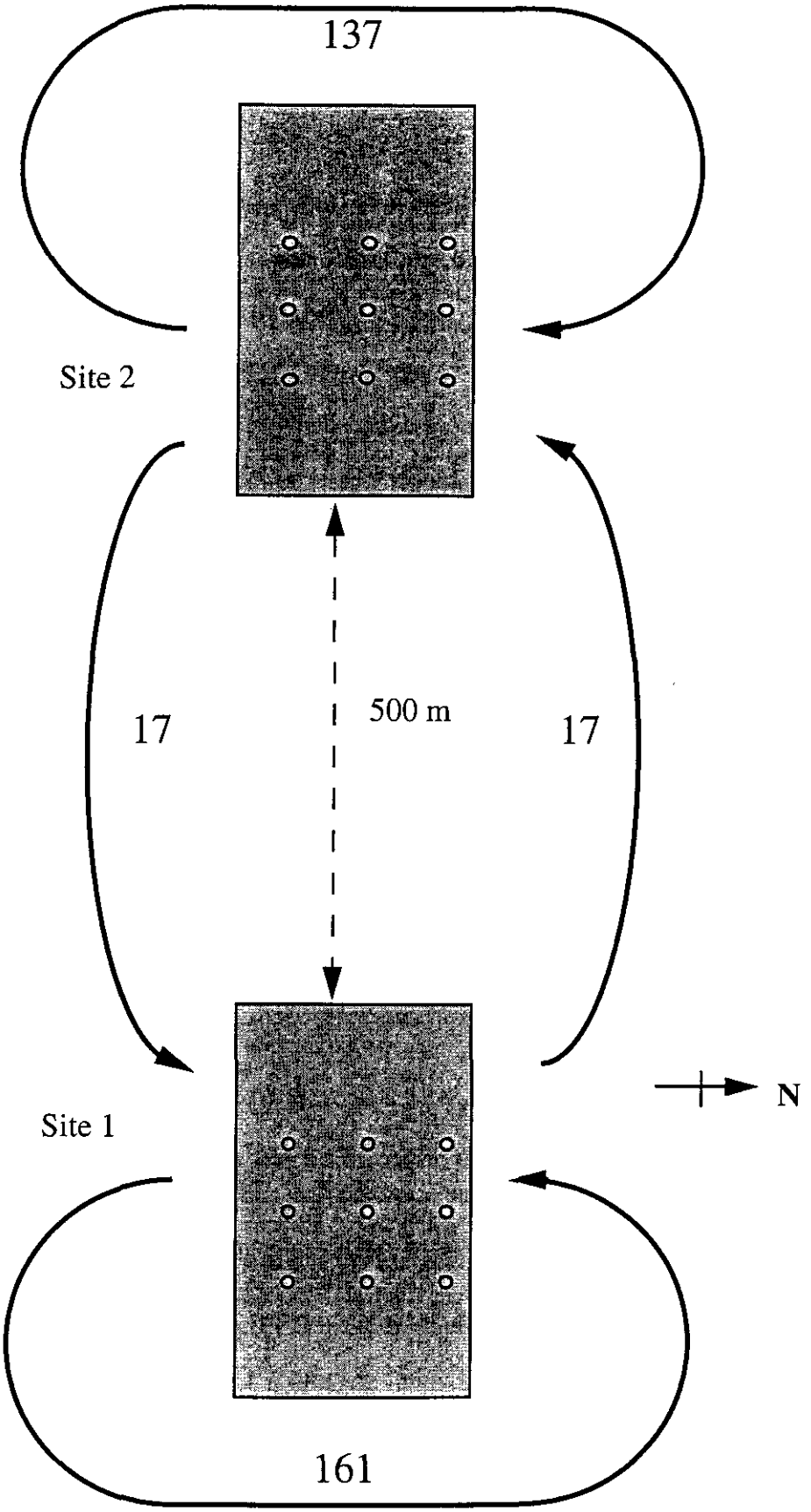
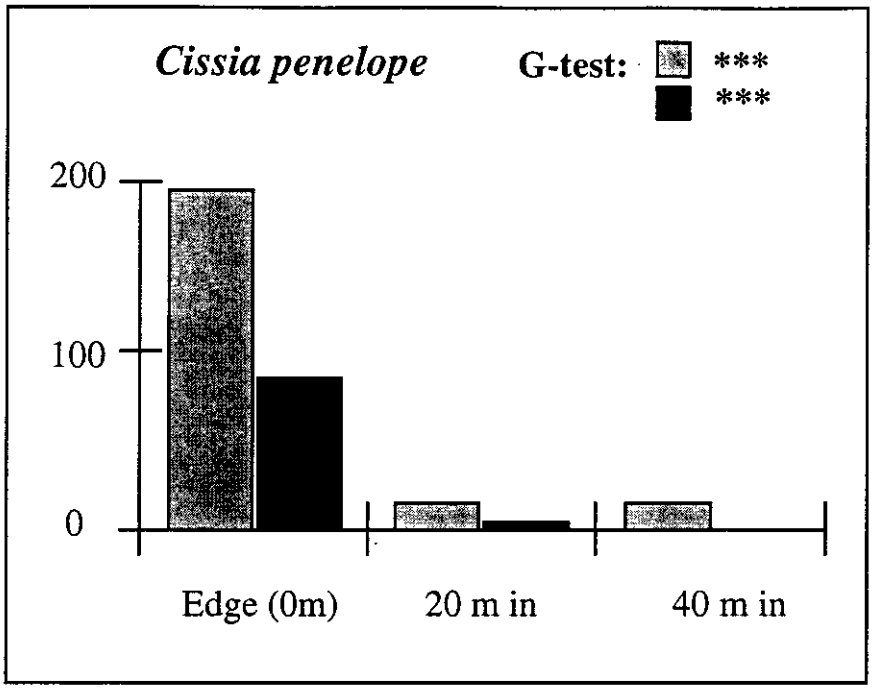


Figure 4.3. The total recapture events of all species within and between site replicates in study 1.

Cissia penelope, the most abundant species encountered in the study (35 % of all individuals marked), was found to occur in significantly greater numbers of new captures at the forest edge than either 20 m or 40 m in. This was true for both replicates of the study design ($G = 126.3$, $p<0.001$, $df=2$ and $G = 162.2$, $p<0.001$, $df=2$). The combined replicate results are shown here (Fig. 4.4.a). *Cissia hermes* also showed this distribution pattern ($G = 67.75$, $p<0.001$, $df=2$, Fig. 4.4.b). Conversely, certain species, such as *Colobura dirce* ($G = 15.1$, $p<0.001$, $df= 2$) and *Morpho peleides* ($G = 7.7$, $p<0.05$, $df= 2$) were found in significantly greater numbers 40 m into the forest (Fig. 4.5.a&b). When the *Morpho peleides* data were analysed separately between the two sexes, although most new captures were found 40 m in, neither males nor females were significantly stratified horizontally ($G=4.23$, $df=2$, $p>0.05$ and $G=4.78$, $df=2$, $p>0.05$ respectively). Female *Morpho peleides* recaptures were also not significantly stratified ($G=2.39$, $df=2$, $p>0.05$) but males were stratified ($G=6.8$, $df=2$, $P<0.05$).

No significant difference in horizontal stratification was found for the new captures of all three *Caligo* species combined (*C. teucer*, *C. eurilochus* and *C. illeonus*; $G = 5.34$, $p>0.05$, $df=2$), (Fig. 4.6.a) or for any of the other species encountered with ≥ 15 expected captures between the three categories of edge, 20 and 40 m in; combined *Taygetis* species group ($G = 1.5$, $p>0.05$, $df=2$, Fig. 4.6.b), *Opsiphanes cassina* ($G = 1.5$, $p>0.05$, $df=2$), and *Archaeoprepona demophon* ($G = 1.5$, $p>0.05$, $df=2$).

When patterns of distribution with respect to a forest edge were explored using recapture events for each species with ≥ 15 expected captures between the three categories of edge, 20 and 40 m, significant results were obtained for *C.penelope* ($G =145$, $p<0.001$, $df=2$, Fig. 4.4.a) and *Morpho peleides* ($G = 9.95$, $p<0.01$, $df=2$, Fig. 4.5.b), but not for *Colobura dirce* ($G = 0.177$, $p>0.05$, $df=2$, Fig. 4.5.a). The *Caligo* species data also showed a difference between the capture and recapture event distribution pattern, with significantly more recapture events recorded 20 m into the forest than in the other two strata ($G = 7.77$, $p<0. 05$, $df=2$, Fig. 4.6.a). Insufficient recaptures prevented G-tests from being carried out on the *C.hermes*, *Taygetis*, *O. cassina* and *A. demophon* data.



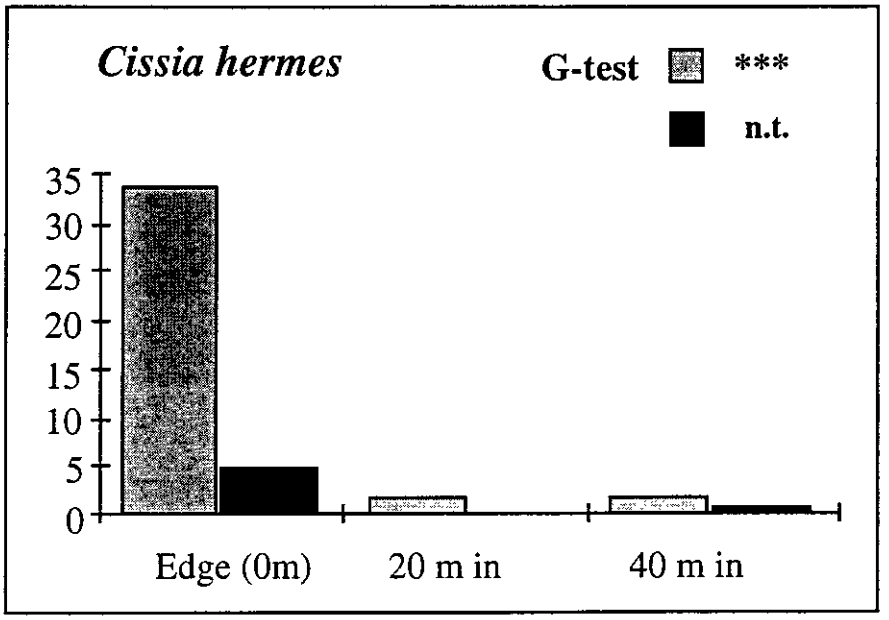
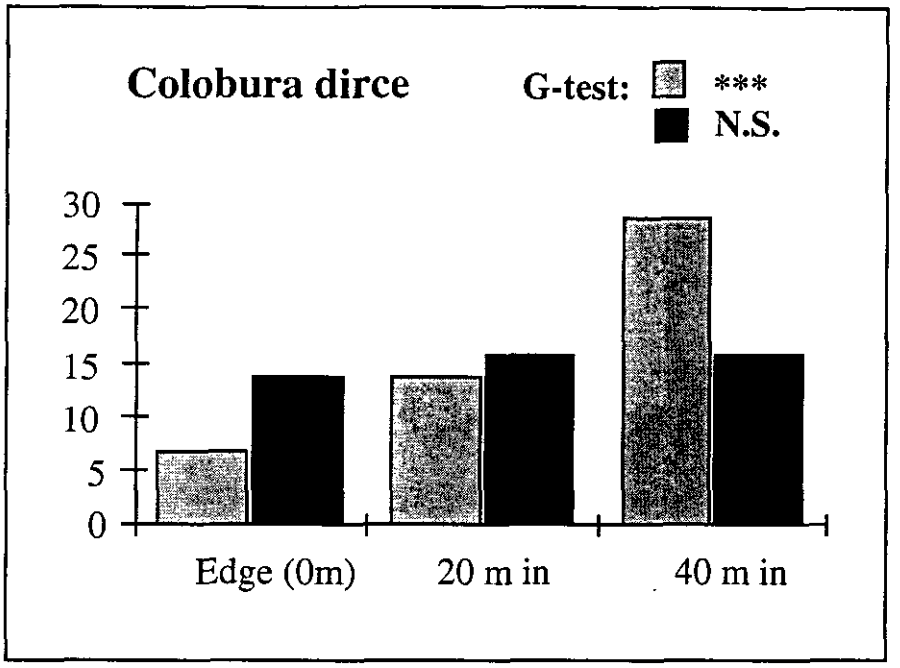


Figure 4.5. The number of captures ▒ and the number of recaptures ■ of **a)** *C. penelope* and **b)** *C. hermes* at the forest edge, 20 m and 40 m into the forest (site 1 and 2 results combined). *** : significance at $p<0.001$, ** : significance at $p<0.01$, * : significance at $p<0.01$, **N.S.**: not significant, $p>0.05$, **n.t.**: not tested as too few data points.



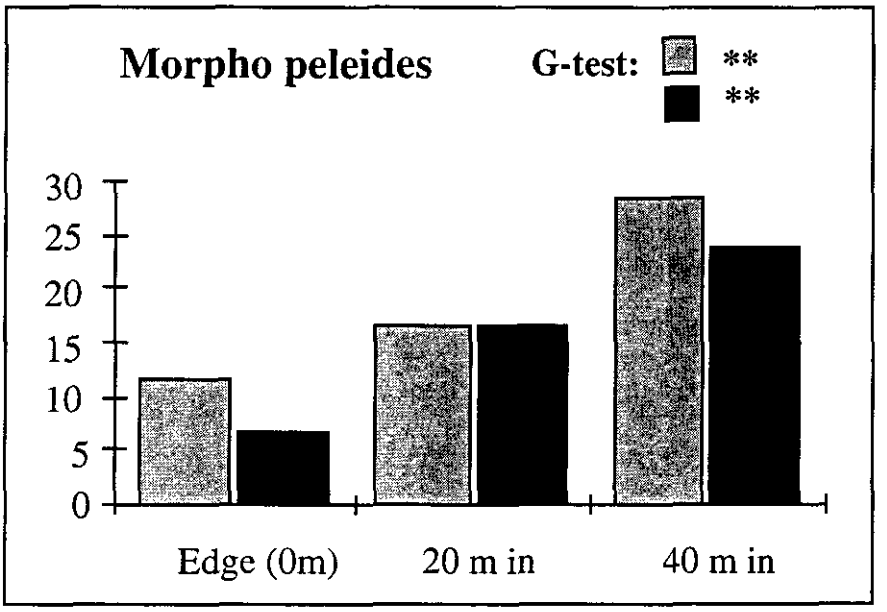
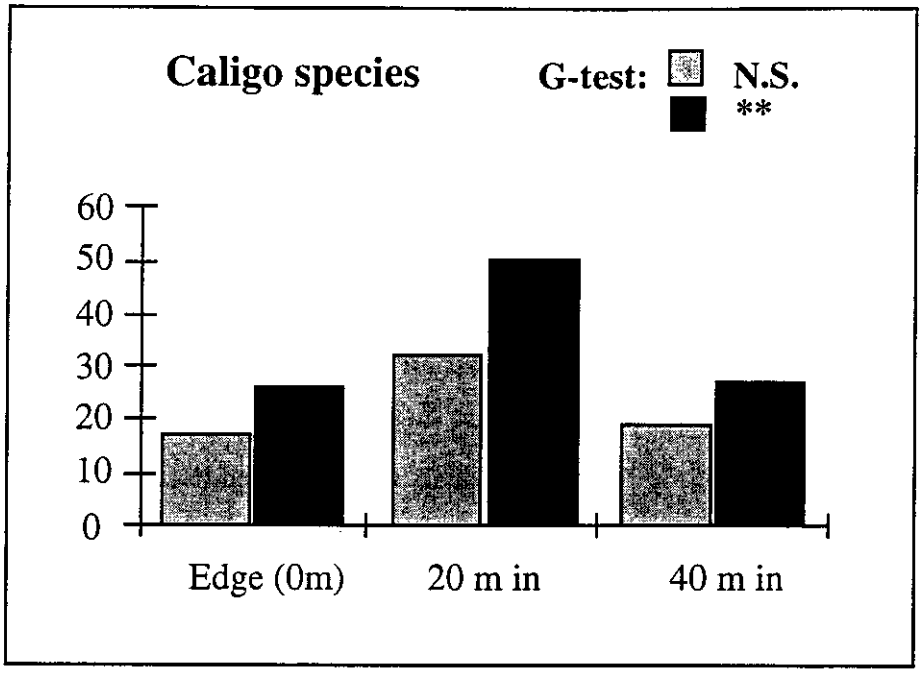


Fig.ure 4.6. The number of captures ▨ and the number of recaptures ■ of **a)** *Colobura dirce* and **b)** *Morpho peleides* at the forest edge, 20 m and 40 m into the forest (site 1 and 2 results combined). *** : significance at $p<0.001$, ** : significance at $p<0.01$, * : significance at $p<0.01$, **N.S.**: not significant, $p>0.05$, **n.t.**: not tested as too few data points.



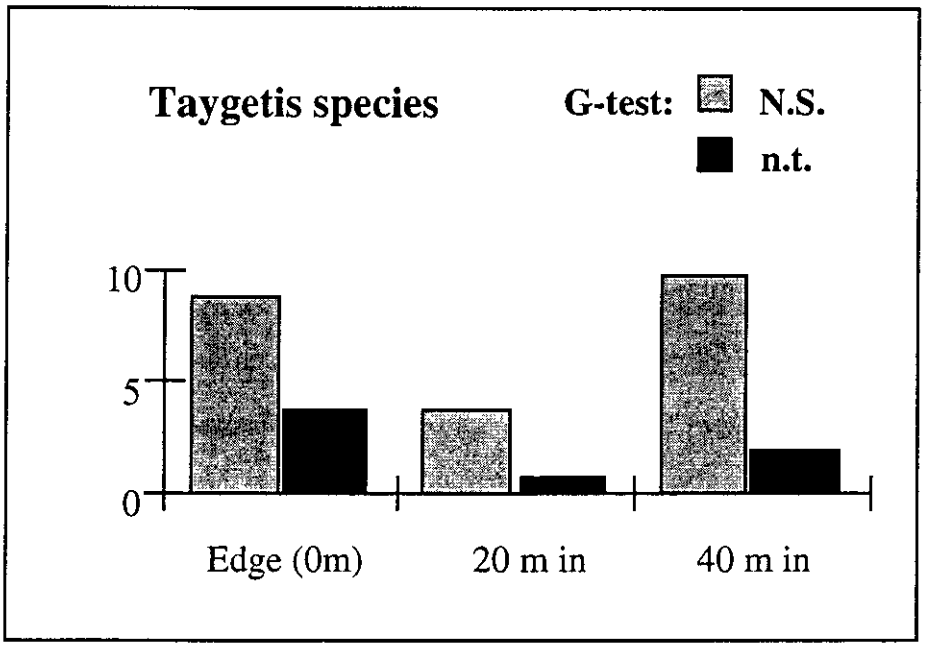


Figure 4.6. The number of captures ▭ and the number of recaptures ■ of three **a)** *Caligo* species and **b)** *Taygetis* species at the forest edge, 20 m and 40 m into the forest (site 1 and 2 results combined). *** : significance at $p<0.001$, ** : significance at $p<0.01$, * : significance at $p<0.01$, **N.S.**: not significant, $p>0.05$, **n.t.**: not tested as too few data points.

Similar comparisons between the number of captures caught in the three sets of traps perpendicular to the forest edge (i.e. each set of three comprising one trap at the forest edge, one 20m in and one 40 m in) were also made. For *C. penelope* at site 1, observed capture totals of 65, 21 and 36 were found to be significantly different from those expected if these captures had been distributed evenly ($G = 24.4$, $p<0.01$, $df=2$). At site 2 there was no difference between observed (40, 42 and 33) and expected (38.33) totals of captures ($G = 1.2$, $p>0.05$, $df=2$). For *Morpho peleides* there was no significant difference at either site ($G = 2.96$, $p>0.05$, $df=2$ at site 1 and $G = 0.55$, $p>0.05$, $df=2$ at site 2). *Colobura dirce* showed no difference at site 1 ($G = 0.28$, $p>0.05$, $df=2$) but showed significantly fewer individuals were captured in one set of three traps than the other two (5, 15 and 13 individuals, $G = 5.76$, $p<0.05$, $df=2$). When the results were combined for site 1 and 2 for *C. penelope*, *C.hermes, Morpho peleides* and *Colobura dirce*, there was only a significant difference between the observed and expected totals for *C. penelope* ($G = 12.6$, $p<0.01$, $df=2$).

Of the 23 species recaptured, representatives of seven of these were recaptured moving the 0.5 km between the site replicates, comprising 29 individuals and 34 recapture events (17 recapture events each way between the sites, Fig. 4.3). These species were *C. penelope* (11 individuals; 15.7% of *C. penelope* individuals recaptured), *Caligo* species (seven individuals; 24.1 %), *Colobura dirce* (three individuals; 12 %), *Morpho peleides* (three individuals: 12 %), *C. hesione* (two individuals; 100 %), *Archaeoprepona demophon* (two individuals; 100 %) and *Catoblepia berecynthia* (one individual; 33.3 %).

4.3.2. Study 2: movement across breaks in the forest

Over the five weeks of this study (23 days trapping), 31 species were encountered (Appendix B.1), 27 of which were represented by more than one individual. In study 2, 1560 individuals were marked, of which 548 individuals were recaptured (35.1 %). Of these 548 individuals, 382 or 70 % of individuals were recaptured moving between traps (166 individuals or 30 %, were recaptured in the same trap that they were first caught in) and 221 individuals were recaptured crossing at least one of the breaks in the forest (58 % of individuals recaptured moving between traps; Table 4.1).

The distribution of new captures between north and south-facing forest strata (Fig. 4.7), revealed that significantly higher numbers were found at north-facing than south-facing edges (387 vs 174 for forest blocks, $G = 82.9$, $p<0.0001$, $df=1$ and 568 vs 226 for forest strip, $G = 152.2$, $p<0.0001$, $df=1$), with similar ratios of 2.22 and 2.51 more captures in these north-facing edges, respectively.

This was investigated further by plotting out the movement patterns (or recapture movements) within and between the forest blocks as shown in Figure 4.8.a, the movement patterns of all species combined together. This showed no significant net flow of individuals in either direction, the total number of recaptures heading north (left to right at the top of the figure) was found to be 150, compared with 156 recaptures heading south. When the number of recapture events within forest blocks was expressed as a ratio of the total recapture events related to each block (i.e. total recapture events within the block plus those leaving and entering each respective blocks), the ratios obtained of 0.65 (379 / 585) for the southernmost block , 0.65 (503 / 771) for the strip forest and 0.50 (136 / 274) for the northern block were found to be not significantly different from one another ($G=2.71$, $df=2$, $p>0.05$, Fig. 4.8.a). When only the recapture events of *C. penelope* individuals were analysed (Fig. 4.8.b), the ratios of 0.57, 0.65 and 0.25, respectively, were found to be significantly different from one another ($G=20.62$, $df=2$, $p<0.05$).

Table 4.1. A list of the species which crossed one or both of the breaks between the forest blocks, those which were recaptured but did not cross a break, and those which were not recaptured in study 2. * *Taygetis echo* is a black butterfly and proved difficult to mark uniquely so individuals encountered were either marked or unmarked. Hence there were either three recaptures (three individuals) or one recapture and three recapture events.

SPECIES	Number individuals marked	Number individuals recaptured	No. individuals crossed break (% of recaptures)
Recaptured & crossed			
Cissia penelope	893	340	162 (47.6 %)
C. hermes	102	11	1 (9.1 %)
C. hesione	42	17	5 (29.4 %)
C. myncea	37	12	4 (33.3 %)
Caligo eurilochus	33	23	9 (39.1 %)
Caligo teucer	45	22	8 (36.4 %)
Catoblepia berecynthia	12	5	1 (20 %)
Colobura dirce	70	18	6 (33.3 %)
Morpho peleides	70	39	17 (43.6 %)
Opsiphanes cassiae	5	1	1 (100 %)
Taygetis andromeda	76	24	5 (20.1%)
T. virgilia	23	7	2 (28.6 %)
Recaptured, not crossed			
Cissia arnaea	6	2	0
C. themis	3	2	0
Caligo illeonus	6	3	0
Eryphanis automedon	3	2	0
Hamadryas feronia	19	3	0
Opsiphanes cassina	2	1	0
Pierella hyalinus	4	1	0
Taygetis echo	5	1-3*	?
T. penelea	8	2	0
Not recaptured			
Archaeoprepona demophon	3	0	-
A. demophoon	1	0	-
Adelpha iphicla	3	0	-
Biblis hyperia	1	0	-
Cissia cephus	1	0	-
C. libye	1	0	-
C. renata	5	0	-
C. terrestris	3	0	-
Historis acheronta	1	0	-
Ithomia pellucida	3	0	-

Of the 31 species encountered, 21 were recaptured, of which 12 were recaptured having crossed one or both of the breaks between forest blocks. For example, 48 % of recaptured *Cissia penelope* individuals crossed the road, 44 % of recaptured *Morpho peleides* and 33 % of recaptured *Colobura dirce* individuals (Table 4.1). Nine other species were recaptured, but not across a break. For all of these nine species, however, the number of individuals captured (between two and 19 individuals) and recaptured (between one and seven individuals) were low. The remaining 10 species were not

recaptured at all.

The movement patterns of the five most abundant species trapped in this study (*C. penelope*, *C. hermes*, *Morpho peleides*, *Caligo* species and *Colobura dirce*) are displayed as numbers of movements with respect to each stratum of fruit traps (Figs. 4.9.a-e). *Cissia penelope* individuals were recorded making 840 recapture events in study 2 (Fig. 4.9.a). The vertical arrow in each of the six diagrams in this figure, depicts the total number of recaptures along that forest stratum. In the top diagram, for example, there were four recaptures of *C. penelope* 40 m into the forest. These were either recaptures between the three traps in this stratum or recaptures in the same trap. The other arrows and numbers represent the number of recapture events from the traps in this stratum. Hence six were recaptured at the north-facing edge 40 m away, five were recaptured at the south-facing edge 80 m away having crossed the road break, and so on. This figure clearly reinforces the preference of movement *C. penelope* appeared to have along the two north-facing forest edges. Similar figures show these movements for *Morpho peleides*, *Cissia hermes*, *Colobura dirce* and the *Caligo* species (Figs. 4.9.b-e).

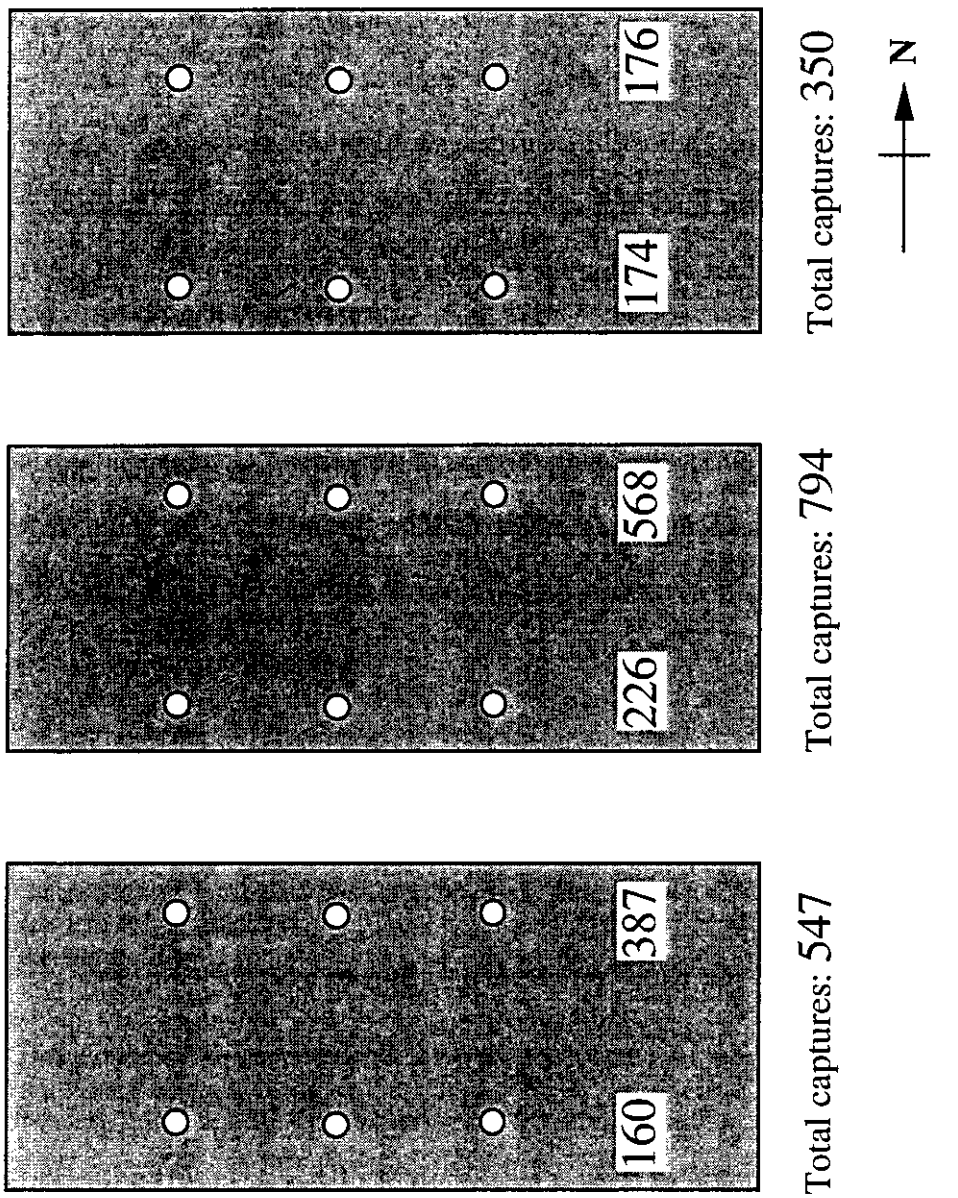


Figure 4.7. Distribution of total numbers of new captures for individuals of all species captured in study 2

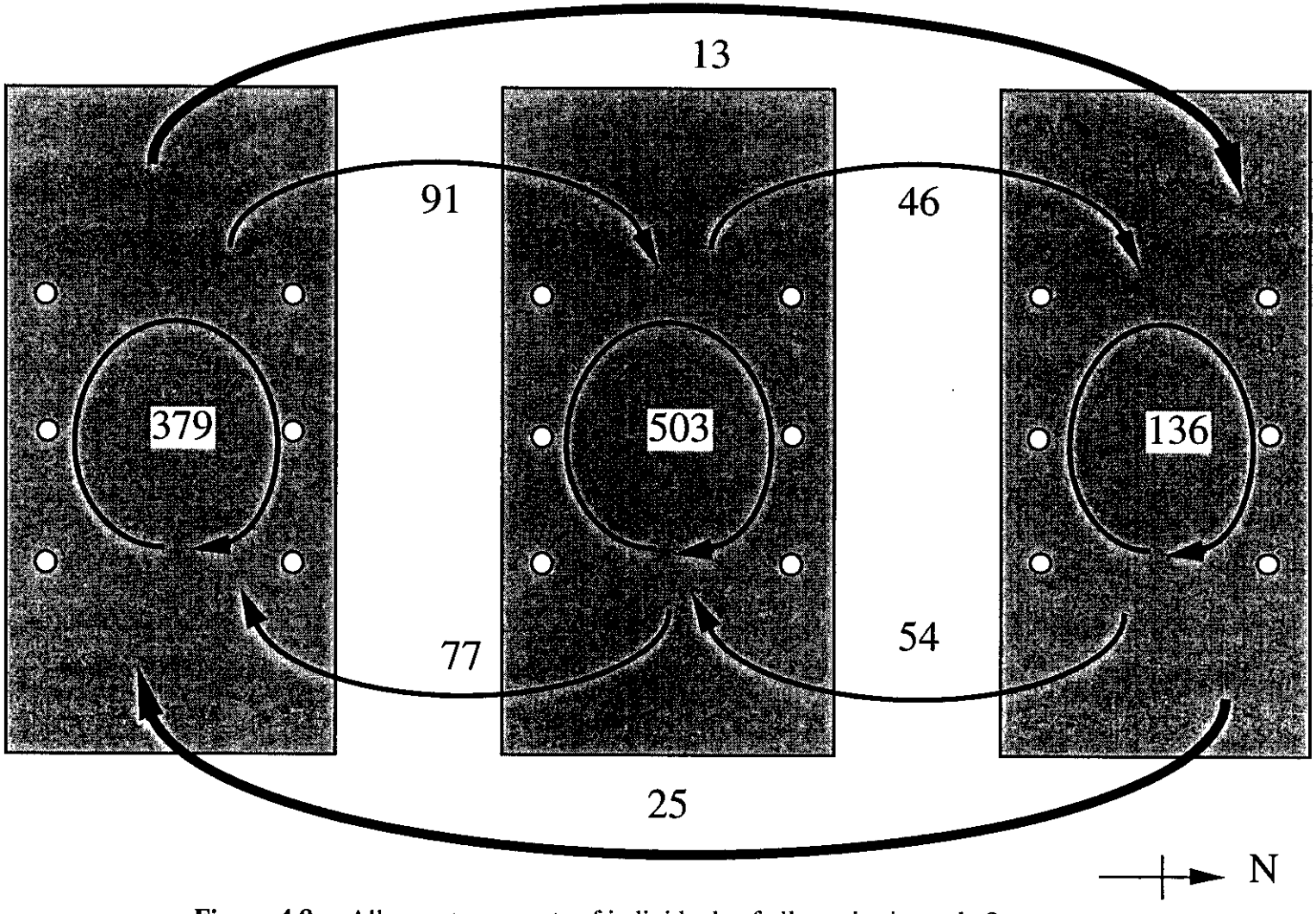


Figure 4.8.a. All recapture events of individuals of all species in study 2.

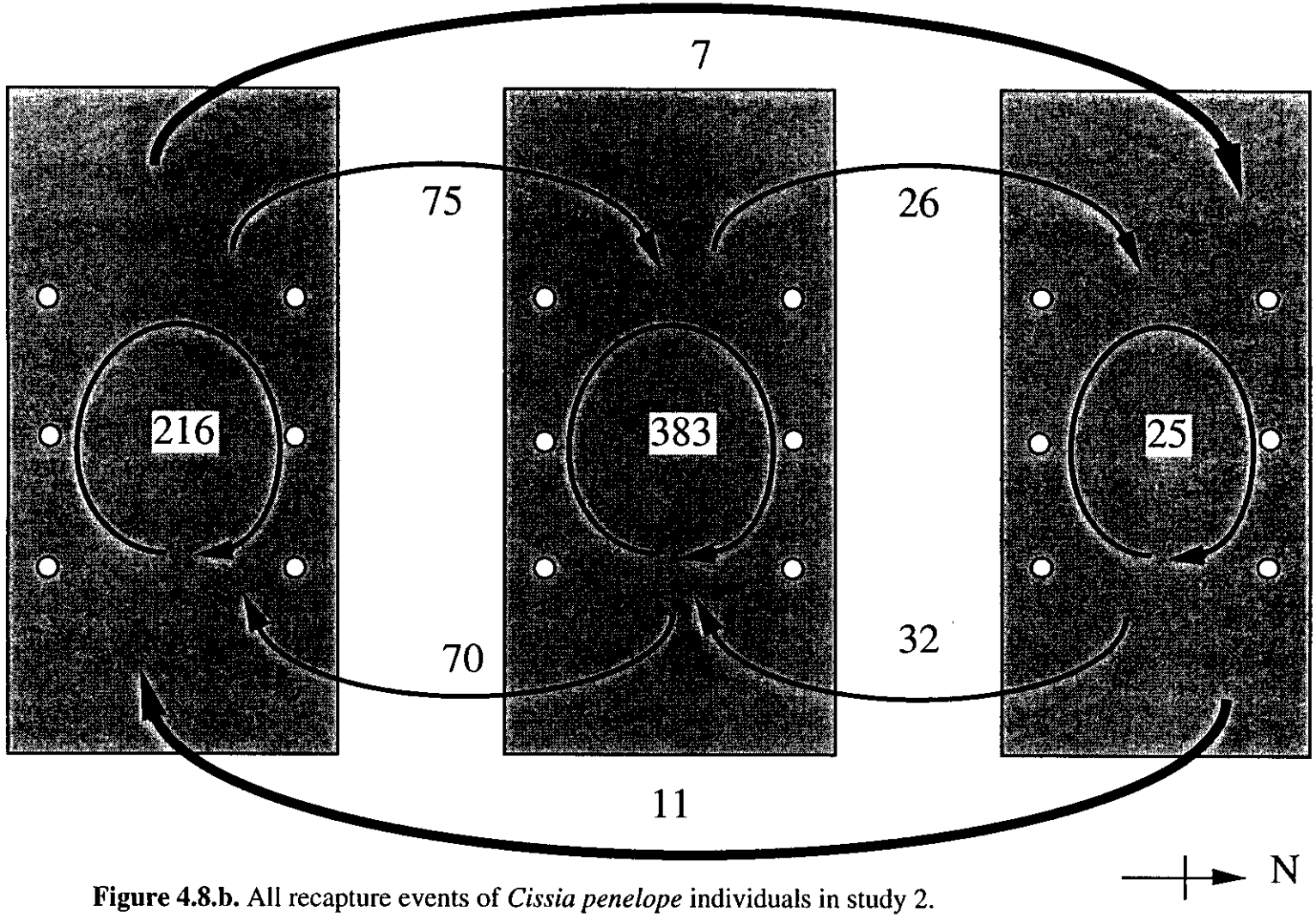


Figure 4.8.b. All recapture events of *Cissia penelope* individuals in study 2.

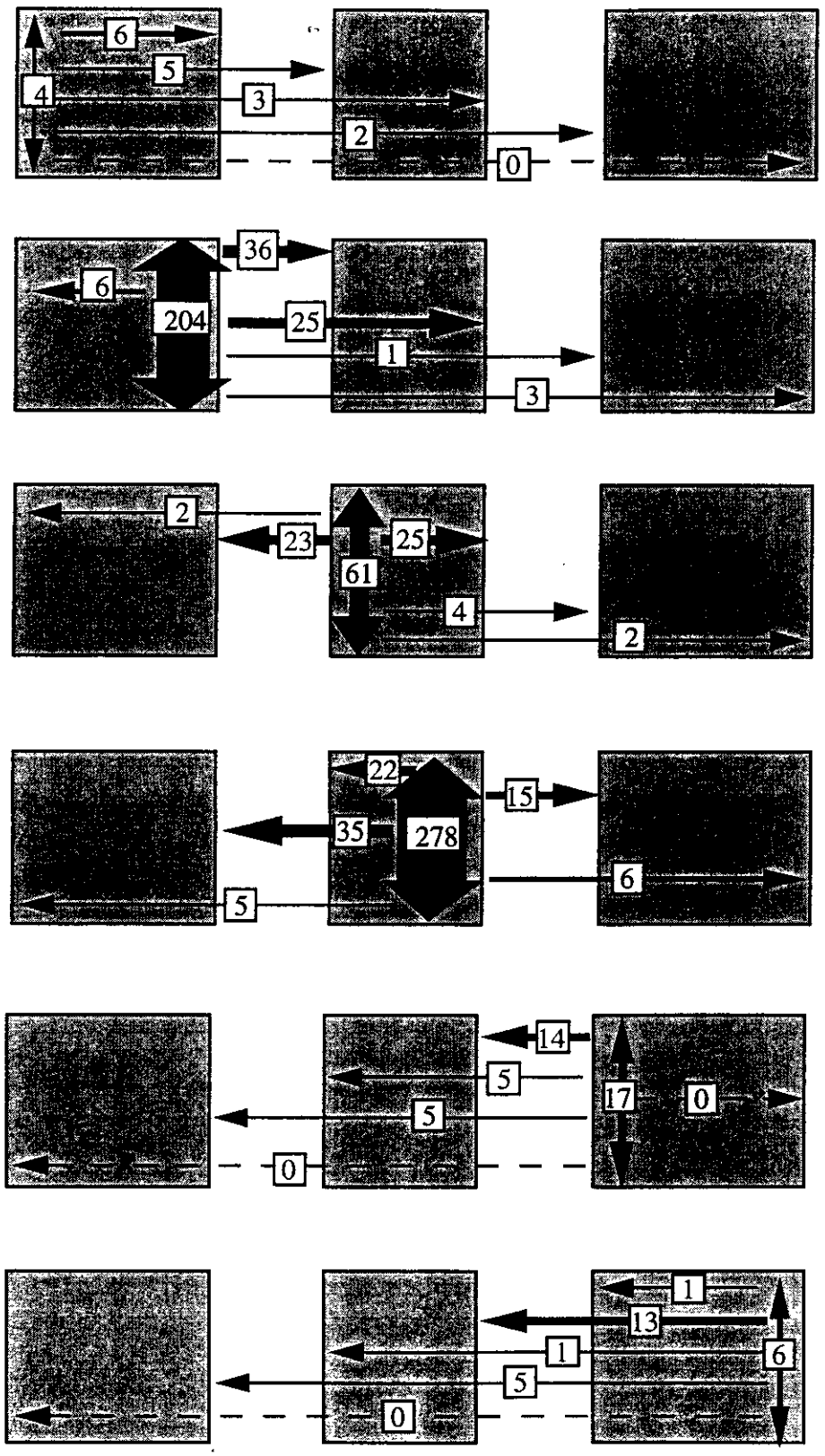


Figure 4.9. a. Recapture events along (including same trap recaptures) and from each forest stratum for *Cissia penelope*.

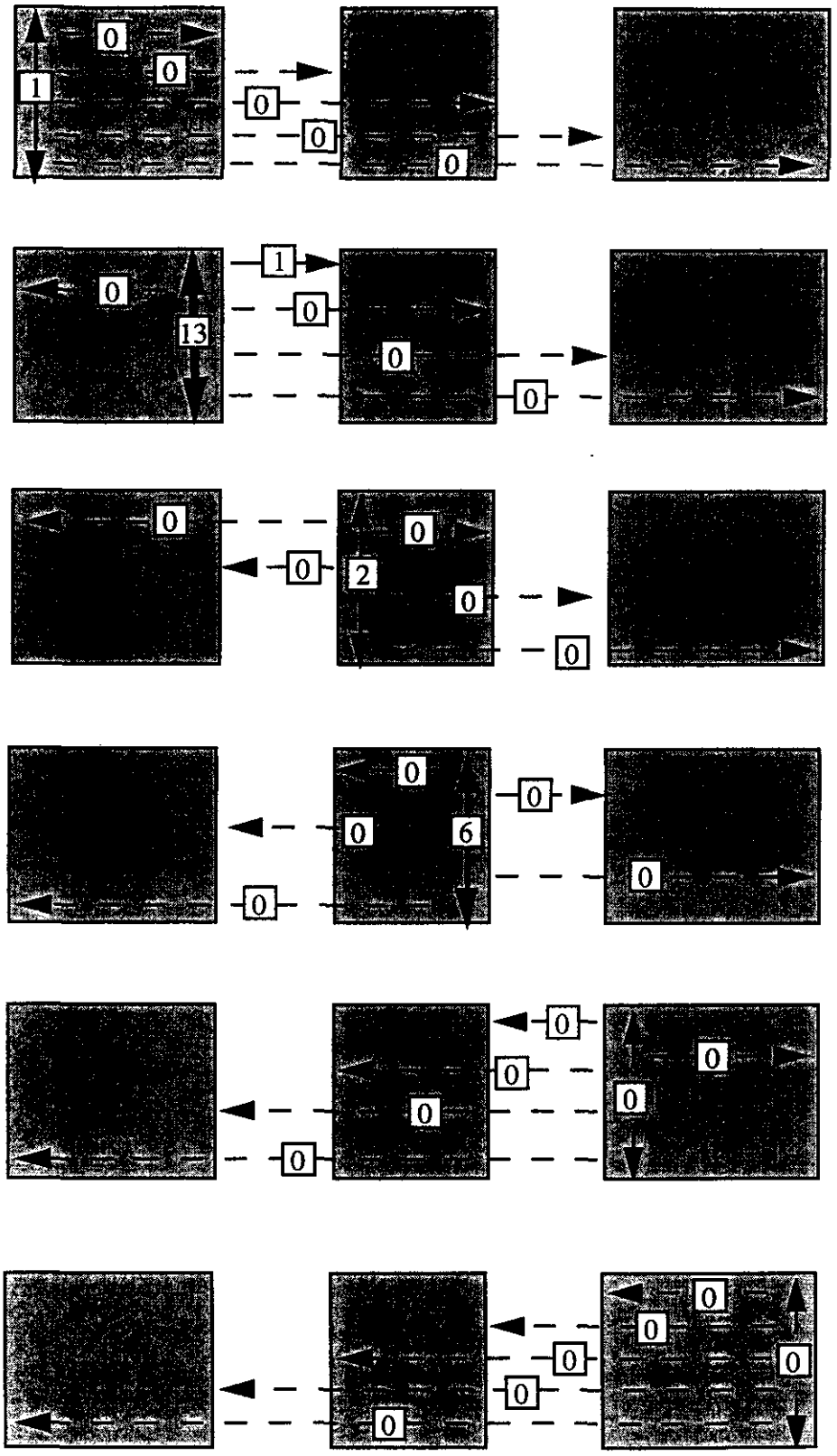


Figure 4.9. b. Recapture events along (including same trap recaptures) and from each forest stratum for *Cissia hermes*.

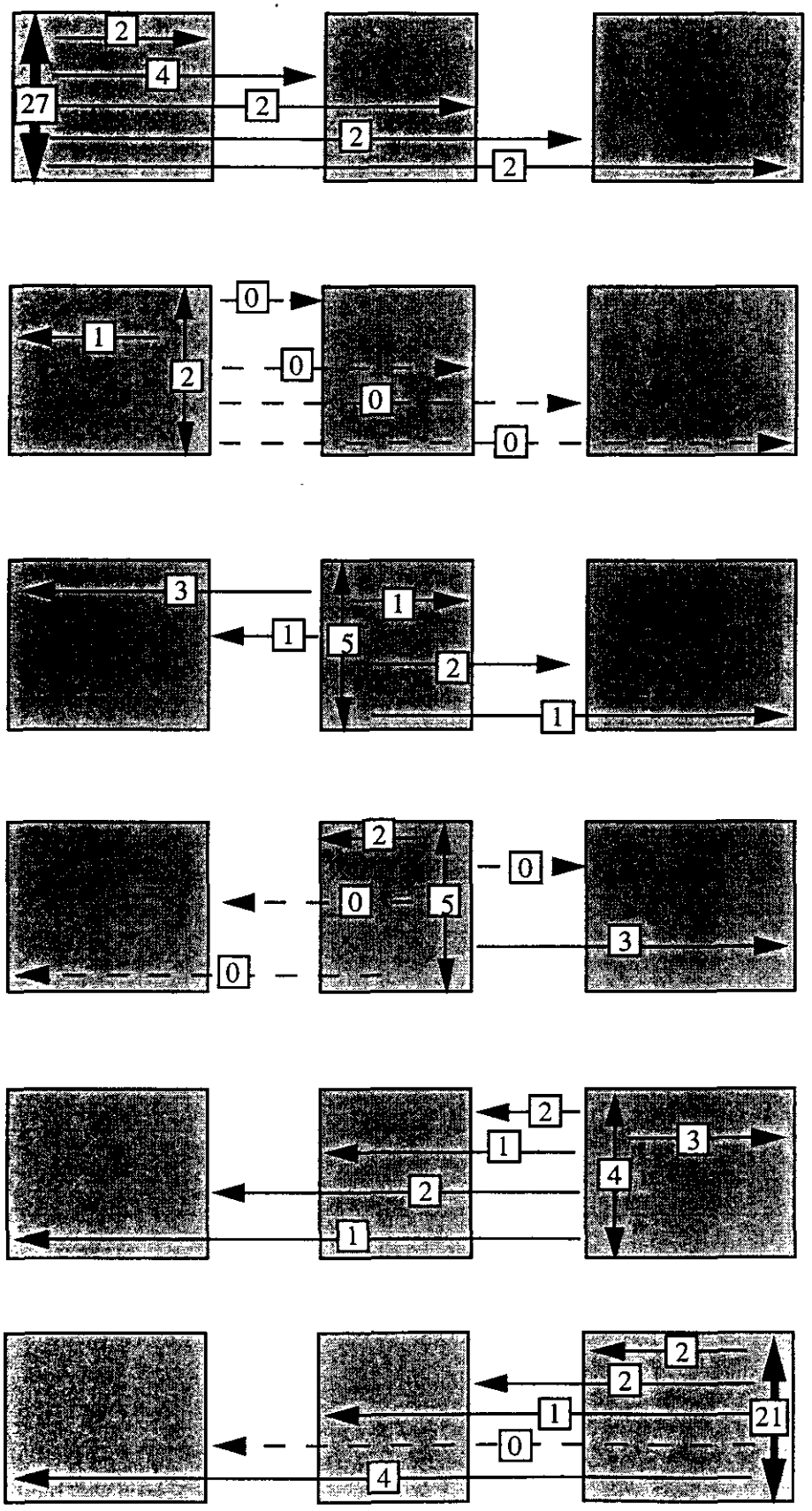


Figure 4.9. c. Recapture events along (including same trap recaptures) and from each forest stratum for *Morpho peleides.*

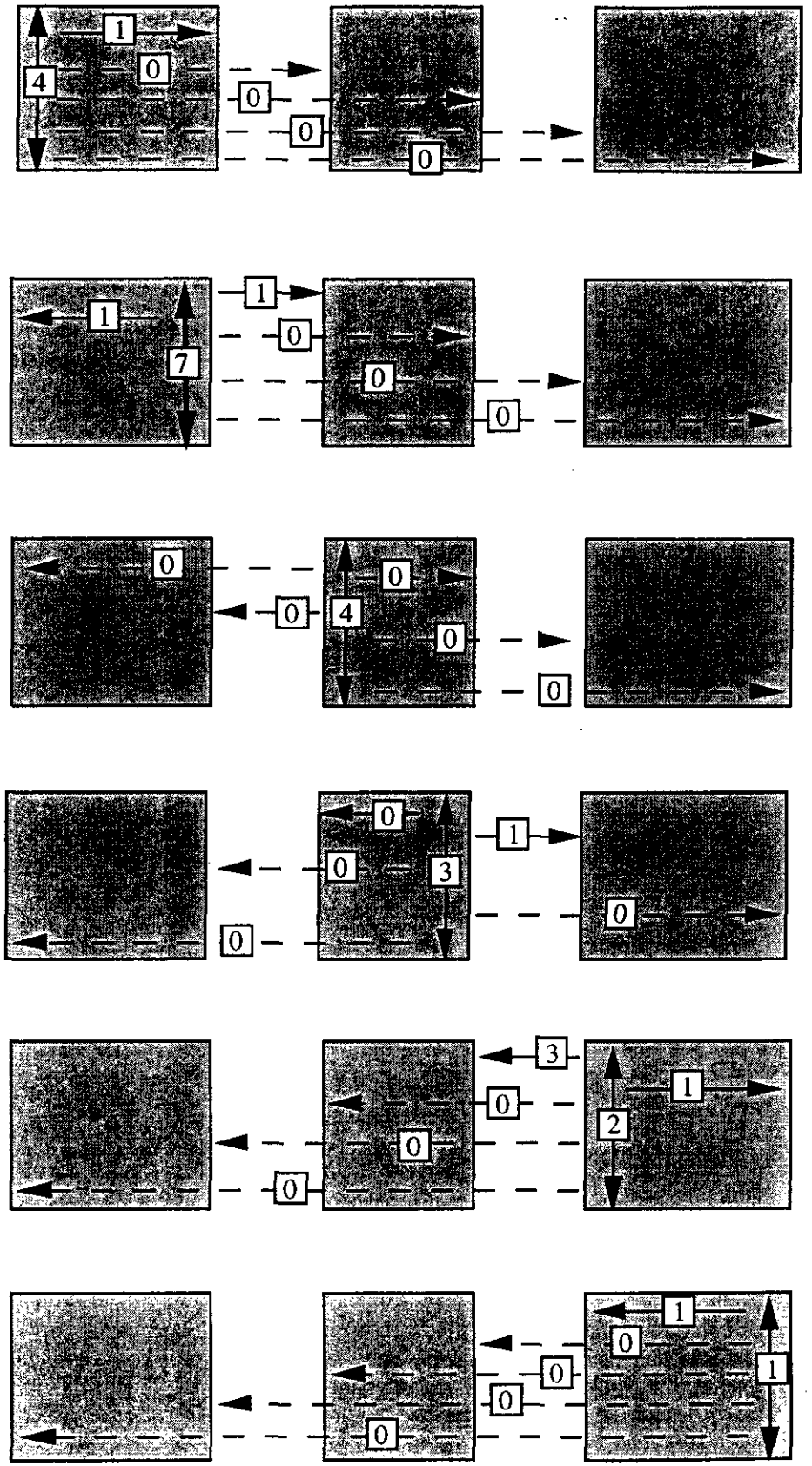


Figure 4. 9. d. Recapture events along (including same trap recaptures) and from each forest stratum for *Colobura dirce*.

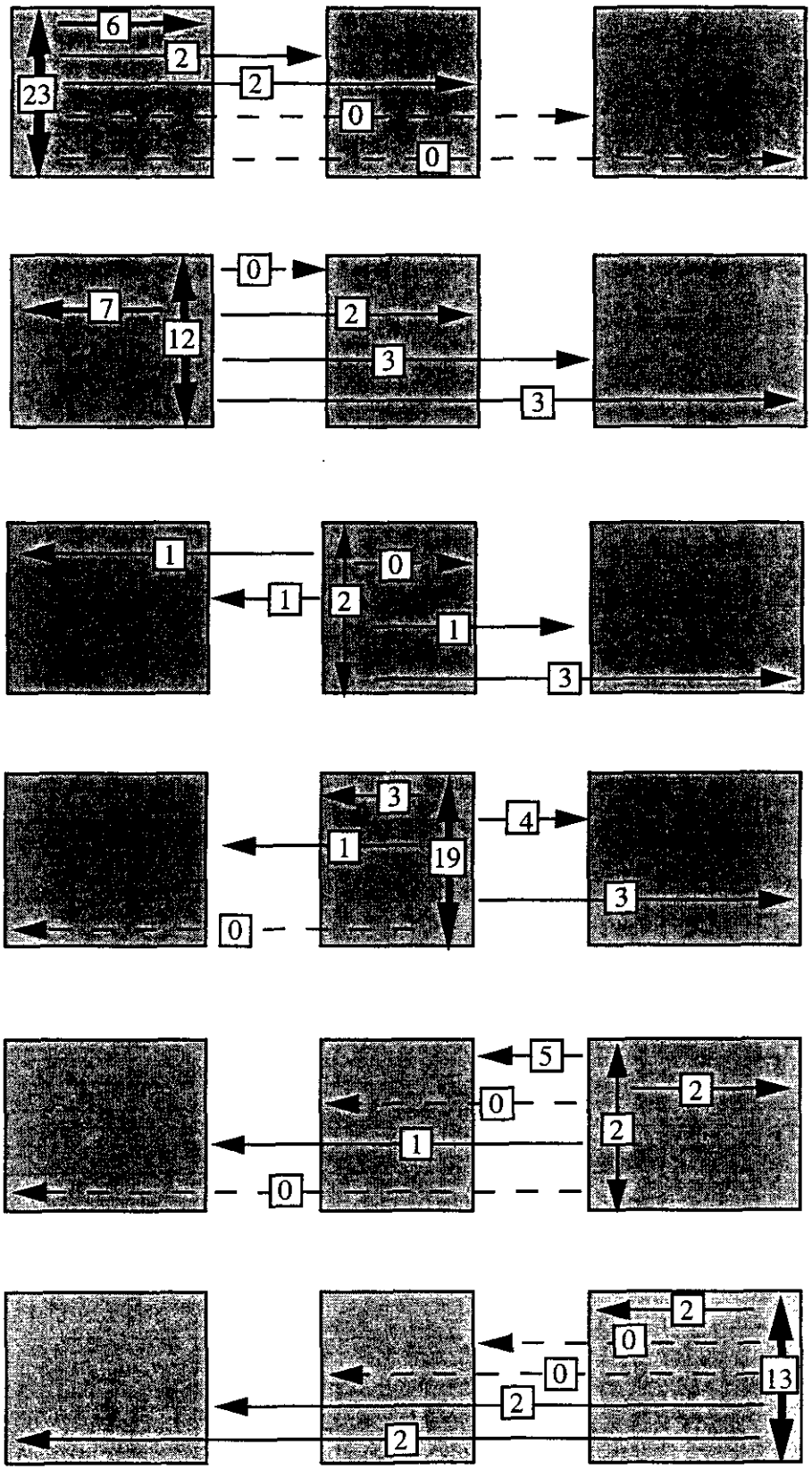


Figure 4.9. e. Recapture events along (including same trap recaptures) and from each forest stratum for the *Caligo* species.

When number of observed road and gas-line crossings (in terms of (a) recapture events and (b) individuals) were compared with the expected number of crossings (from Munguira and Thomas, 1992), it was seen that for the two species with expected values greater than five which allowed significance testing, *C. penelope* and *Morpho peleides*, there was no significant difference between observed and expected crossings of the road or the gas-line, for number of recapture events or individuals (Table 4.2.b). The number of new captures used to generate the observed and expected number of crossings in Table 4.2.b are shown in Table 4.2.a. When the number of road and gas-line crossings were pooled, it was still found that there was no significant difference between the number of observed crossings of a gap (either road or gas-line) and those expected (Table 4.2.c).

When these data were broken down even further, to look at movements within the forest blocks as well as across the road and gas-line, again no significant differences were found between the number of observed movements (either (a) recapture events or (b) number of individuals) and those expected from Munguira and Thomas (1992). Although observed and expected values were also given for *Morpho peleides*, *Caligo* species and *Colobura dirce*, only *C. penelope* generated sufficient data for significance testing.

Table 4.2.a. Totals of new captures in each forest block from which recaptures and observed and expected number of crossings in Table 4.2.b originate.

Species	Totals of new captures			
	Across road		Across gas-line	
	South forest	Strip forest	Strip forest	North forest
C. penelope	107	213	199	35
Morpho peleides	21	9	9	19
Colobura dirce	8	6	5	7
C. hermes	7	3	3	1
C. hesione	6	9	10	1
C. myncea	3	6	5	4
T. andromeda	2	11	13	9
H. feronia	1	2	2	0

Table 4.2.b. Number of individuals recaptured having crossed the road and gas-line in study 2. Data come from captures and subsequent recaptures from the six traps in each forest block. Some individuals were recaught several times, moving between traps and crossing the road or gas-line more than once. These "recapture events" are recorded in row **a** for each species. Row **b** on the other hand, scores individuals as moving or not moving and crossing or not crossing the road or gas-line, irrespective of the number of times it does so. The expected values were calculated using the formula from Munguira & Thomas (1992) (see text).

Species		Recs.	Road crossings		G-test	Recs.	Gas-line crossings		G-test
			Obs.	Exp.			Obs.	Exp.	
C. penelope	a	367	145	163.4	1.1 NS	217	55	55.2	0.0004 NS
	b	223	111	99.3	0.7 NS	149	49	37.9	1.42 NS
Morpho peleides	a	30	12	12.6	0.01 NS	31	14	13.5	0.008 NS
	b	19	9	7.98	0.06 NS	18	11	7.85	0.53 NS
Colobura dirce	a	6	2	2.94	-	10	5	4.06	-
	b	5	2	2.45	-	8	5	3.89	-
C. hermes	a	11	1	4.62	-	1	0	0.38	-
	b	6	1	2.52	-	1	0	0.38	-
C. hesione	a	7	2	3.36	-	7	3	1.16	-
	b	7	2	3.36	-	6	3	0.99	-
C. myncea	a	4	0	1.77	-	8	4	3.95	-
	b	3	0	1.33	-	7	4	3.46	-
T. andromeda	a	3	1	0.78	-	10	7	4.83	-
	b	2	1	0.52	-	6	4	2.9	-
H. feronia	a	0	0	0	-	0	0	0	-
	b	0	0	0	-	0	0	0	-

Table 4.2.c. Combined values for road and gas-line crossings

Species		Road crossings		G-test
		Observed	Expected	
C. penelope	**a**	200	218.6	0.827 NS
	b	160	137.17	1.76 NS
Morpho peleides	**a**	26	26.12	0.0003 NS
	b	20	15.83	0.486 NS
Colobura dirce	**a**	7	7	0 NS
	b	7	6.34	0.033 NS
C. hermes	**a**	1	4.995	-
	b	1	2.895	-
C. hesione	**a**	5	4.52	-
	b	5	4.35	-
C. myncea	**a**	4	5.72	0.31 NS
	b	4	4.79	-
T. andromeda	**a**	8	5.61	0.422 NS
	b	5	3.42	-
H. feronia	**a**	0	0	-
	b	0	0	-

Table 4.3.a. Totals of new captures for each set of three fruit traps at the forest edge (or 40 m into the forest) from which recaptures and observed and expected number of crossings in Table 4.3.b originate.

Species	South forest		Road		Strip forest		Gas-line		North forest	
	forest	N edge	N edge	S edge	S edge	N edge	N edge	S edge	S edge	forest
C. penelope	10	89	101	45	51	151	153	20	13	6
Morpho peleides	17	1	1	7	5	6	4	8	7	9
Colobura dirce	3	4	3	1	2	4	3	5	3	2

Table 4.3.b. Number of (**a**) recapture events and (**b**) number of individuals recaptured having crossed the road, crossing the gas-line and moving between traps within the forest in study 2. Data come from captures and subsequent recaptures between sets of three traps, spaced 40 m apart. Only 4 species had enough data for this break down of movements. The expected values were calculated using the formula from Munguira & Thomas (1992) (see text). Recaptures (**R**), Observed (**O**), Expected (**E**) and G-test value between observed and expected values.

			SPECIES		
			Cissia penelope	*Morpho peleides*	*Colobura dirce*
within forest (S)	**a**	**R**	87	17	3
		O	11	4	2
		E	15.8	1.78	1.47
		G-test	0.864 NS		-
	b	**R**	54	11	3
		O	11	4	2
		E	9.81	1.15	1.47
		G-test	0.068 NS		-
across road	**a**	**R**	156	3	2
		O	67	2	1
		E	66.52	0.66	0.75
		G-test	0.002 NS		-
	b	**R**	94	3	2
		O	53	2	1
		E	40.1	0.66	0.375
		G-test	1.8 NS		-
within strip forest	**a**	**R**	159	4	1
		O	57	3	0
		E	60	1.98	0.44
		G-test	0.08 NS	-	-
	b	**R**	113	4	1
		O	48	3	0
		E	42.65	1.98	0.44
		G-test	0.32 NS	-	-
across gas-line	**a**	**R**	126	3	8
		O	33	3	5
		E	25.76	1.33	3.75
		G-test	0.894 NS	-	-
	b	**R**	90	3	7
		O	27	3	5
		E	18.4	1.33	3.28
		G-test	1.64 NS	-	-
within forest (N)	**a**	**R**	11	13	4
		O	2	6	2
		E	4.75	6.4	1.92
		G-test	-	0.013 NS	-
	b	**R**	7	8	4
		O	1	5	2
		E	3.02	3.94	1.92
		G-test	-	-	-

When the relative frequency distributions of distances flown in study 2 by *C. penelope* and *Morpho peleides* were compared (Fig. 4.10), a highly significant difference between the distributions was found (Kolmogorov-Smirnov test, $D=0.147$, $p<0.01$), with relatively more *Morpho peleides* recapture events recorded flying the longer distances and obviously therefore, more *C. penelope* recapture events between the shorter distances (Sokal and Rohlf 1981).

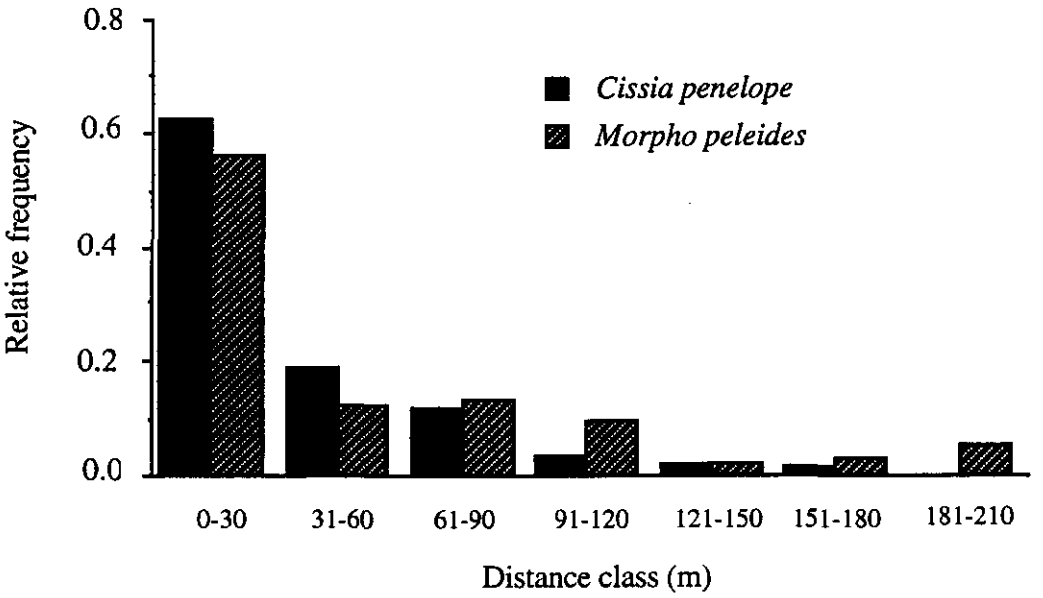


Figure 4.10. Relative frequency of flights made in different distance classes between fruit traps in study 2 for *C. penelope* and *Morpho peleides*

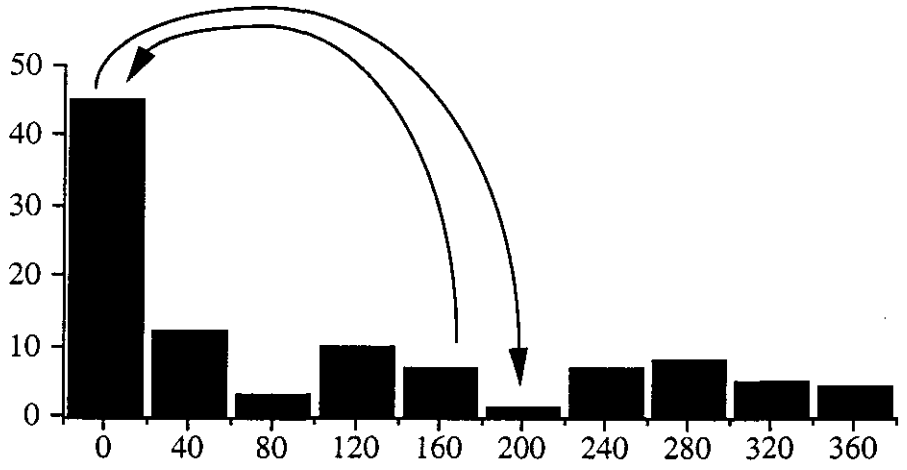
4.3.3. Study 3: movements deeper into the forest

In this 7 day period, 24 species were captured (Appendix B.1), 283 individuals were marked and 44 recaptured (15.5 %). There were 149 recapture events.

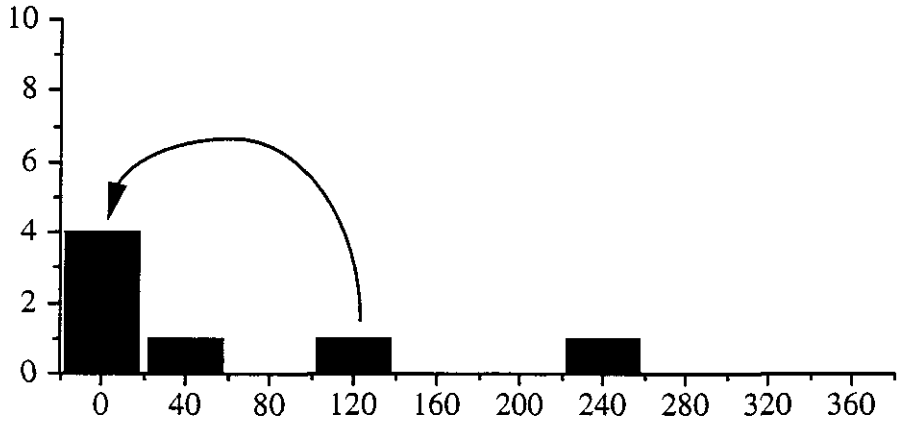
Frequency histograms of number of new captures against distance into the forest (Figs. 4.11.a-i) revealed patterns of stratification that reinforce the patterns observed for several species in study 1 (Sec. 4.3.1). *Cissia penelope*, for example, was much more abundant at the forest edge than at any point deeper into the forest, and *Colobura dirce* was absent at the forest edge (apart from one recapture), but present at all distances deeper into the forest. There appeared to be no difference between the pattern of new captures of *Morpho peleides* males and females. Neither sex were captured at the edge or at 160 m or 200 m into the forest, and were more abundant 40 to 120 m in. The pattern for both sexes mirrored that found in study 2 (sec. 4.3) where there appeared to be stratification and significantly more new individuals captured at 40 m than 20 m or at the forest edge. Only the combined male and female *Morpho peleides* histogram is shown here (Fig. 4.11.e).

Recapture data revealed an individual *C. penelope* which was caught feeding 320 m into the forest, six days after initially having been trapped at the northern forest block edge (study 2) approximately 440 m away (across both the road and gas-line). Another individual was recaught 120 m into the forest in this study, having originally been marked 160 m away across the road in the strip forest edge (study 2). Recaptures of individuals caught in this study are depicted as arrows on the frequency histograms of new captures (Figs. 4.11.a-i), for those species illustrated.

a) *Cissia penelope*



b) *Cissia hesione*



c) *Cissia hermes*

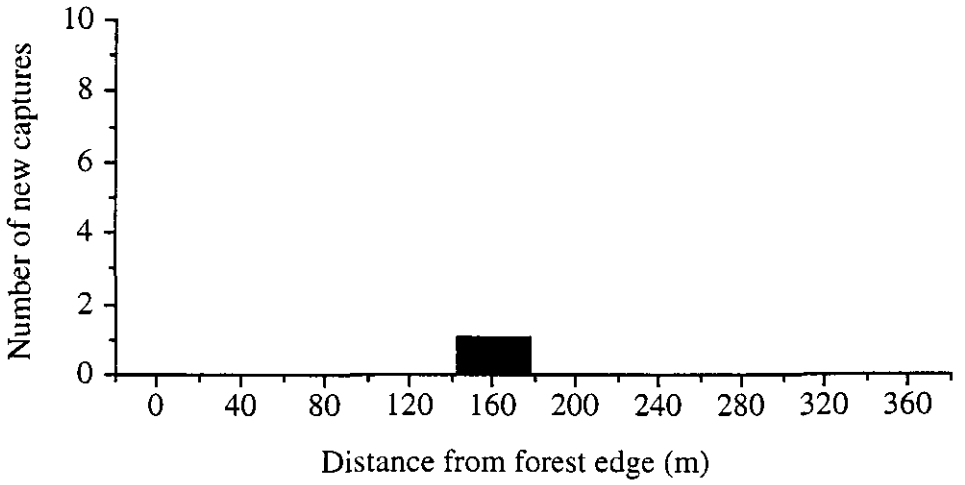


Figure 4.12.a-c. Number of new captures of **a)** *Cissia penelope*, **b)** *C. hesione* and **c)** *C. hermes* in fruit traps in study 3 against distance from the forest edge. The arrows between histogram bars represent individuals recaptured at different distances from their original capture.

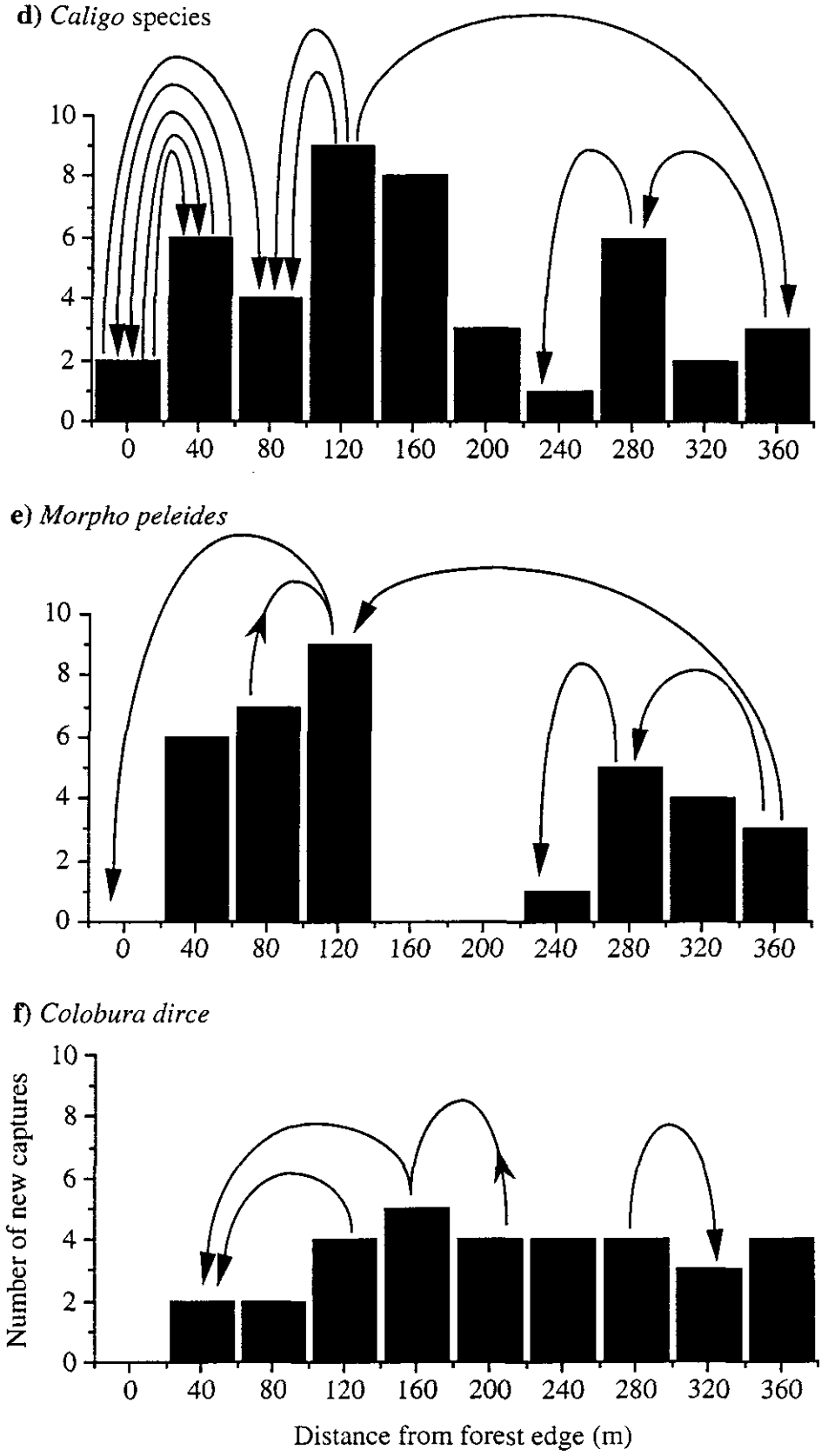
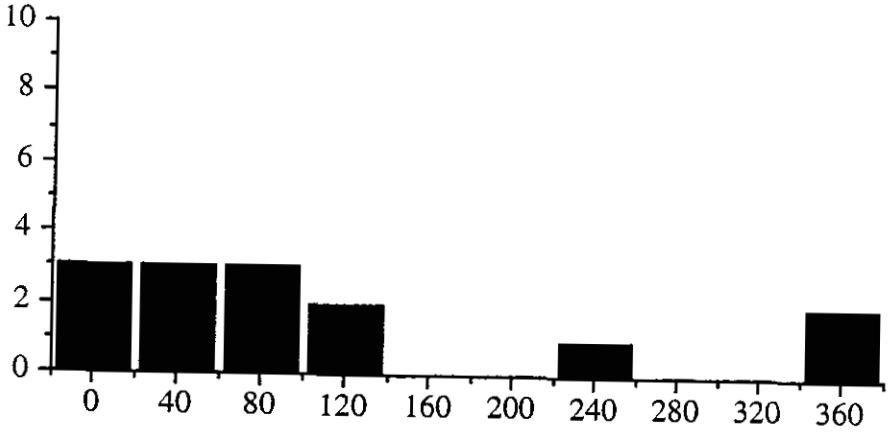
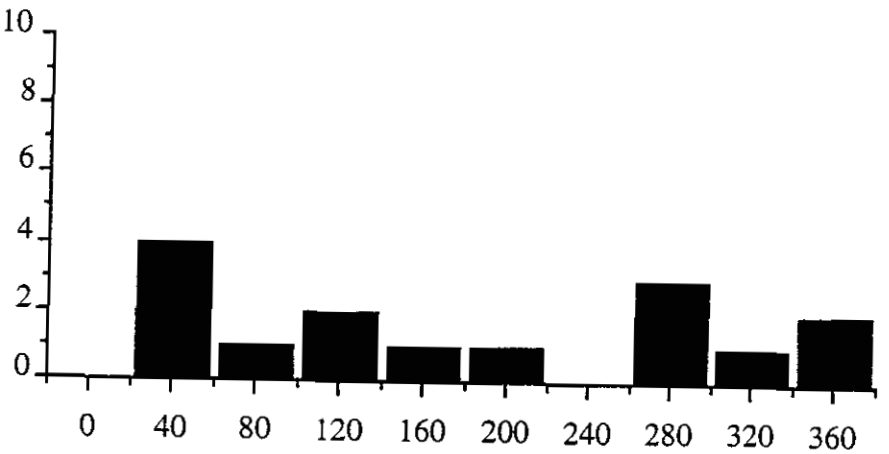


Figure 4.12.d-f. Number of new captures of **d)** the *Caligo* species, **e)** *Morpho peleides* (male and female combined) and **f)** *Colobura dirce* in fruit traps in study 3 against distance from the forest edge. The arrows between histogram bars represent individuals recaptured at different distances from their original capture.

g) *Taygetis andromeda*



h) *T. echo*



i) *T. virgilia*

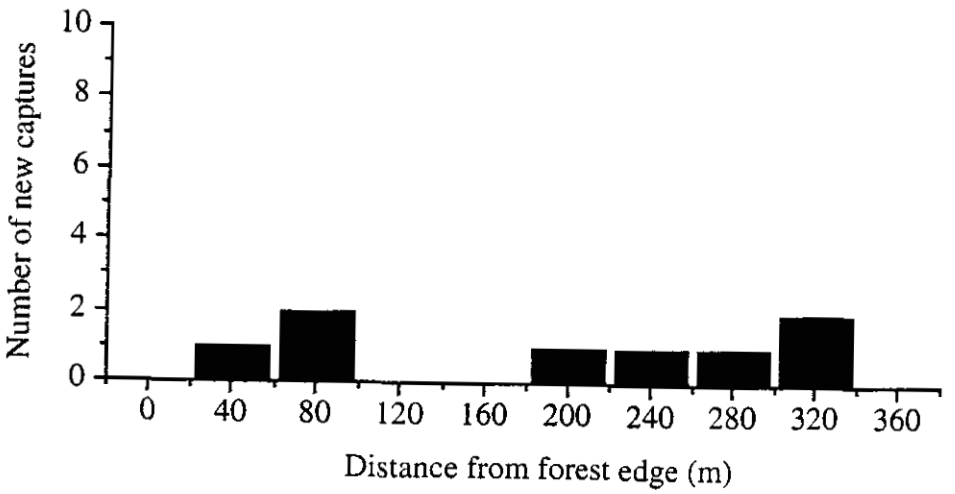


Figure 4.12.g-i. Number of new captures of **g)** *Taygetis andromeda*, **h)** *T. echo* and **i)** *T. virgilia* in fruit traps in study 3 against distance from the forest edge. The arrows between histogram bars represent individuals recaptured at different distances from their original capture.

4.4. Discussion

Several fruit feeding species were found to be horizontally stratified in their distribution from a forest edge to 40 m into forest. The two Satyrinae species, *Cissia penelope* and *C. hermes* were found in greatest abundance at the forest edge and declined in abundance further into forest (Figs. 4.4.a & b). Trapping deeper into forest from the forest edge reinforced this preferred distribution pattern and although individuals were found throughout the 360 m range from edge to interior, they were most concentrated at the forest edge (only one *C.hermes* individual was caught, and not recaptured, in study 3, excluding a comparison of distribution pattern with that observed in study 1). Workers in Manaus, Brazil, reported that most new records of species were found from 100 m of the edge, some at 200 m and occasionally, especially on ridges and small clearings, at 300 m (Brown 1991, Lovejoy *et al.* 1984). Species distributions have been affected by alterations in foodplant distribution in edge habitat. In Kent, U.K., the Heath Fritillary butterfly, *Mellicta athalia*, was found to oviposit the majority of its eggs along the sunny edge of newly cleared woodland where its hostplant, common cow-wheat, *Melampyrum pratense*, was abundant (Warren 1987a, Warren 1987b).

Breaks of 40 m between forest blocks were found to be no barrier to movement of either *C. penelope* or *C. hermes* (although only one *C. hermes* individual was recaptured moving between fruit traps across a break in study 2, many *C. hermes* individuals were observed crossing the breaks). More individuals were found at north-facing edges than south-facing edges, which is likely to be due to north-facing edges being exposed to the daily tracking of the sun. Both these species are host generalists, capable of using a suite of at least 13 grass and sedge species as larval hostplants (Singer and Ehrlich 1993). Emmel (1970) reported that *C.hermes* individuals occupying grassy patches in Costa Rica would peak in flight activity from 7.00 to 9.30 am each morning, and then disappear into the surrounding rubber plantation as the temperature increased. Perhaps this is what is happening here, with *C.penelope* and *C.hermes* individuals using the forest edge habitat to travel along, protected from the sun, foraging for adult resources

and occasionally flying across open habitat to oviposit or to search for other adult resources. Similar distribution patterns were suggested for *C.myncea*, *C.themis*, *C.renata* and *C.hesione*, with *C.hesione* and *C.myncea* individuals occasionally being found in moderate abundance deeper into the forest which may be associated with forest gaps. *C. penelope* has recently been reported to dominate Ecuadorian forest edge habitat (DeVries *et al.* 1997), representing 45 % of captures. Similar patterns of distribution at the forest edge were also reported for *C. hermes* and *C. myncea*.

The opposite pattern of horizontal stratification of highest abundance 40 m into the forest, declining in abundance to the forest edge was observed for two species, *Morpho peleides* and *Colobura dirce* (Figs. 4.5.a & b). These patterns were also found when trapping deeper into the forest, *Colobura dirce* being absent at the forest edge (apart from one recapture), but present at all distances deeper into the forest and *Morpho peleides*, also not captured at the edge (or 160 or 200 m into the forest) but more abundant 40 to 120 m in. Both species were also found to frequently cross breaks in the forest. The larval hostplant of *Colobura dirce* is *Cecropia peltata*, an early pioneer species characteristic of forest gaps and edges. If adult butterfly distribution patterns were solely following hostplant distribution then the opposite distribution to that found for *Colobura dirce* movements would be predicted, i.e. more *Colobura dirce* individuals to be captured at the forest edge, rather than more individuals captured 40 m into forest as found.

The larval hostplant of *Morpho peleides* in Trinidad is a vine, *Paragonia pyramidata* (L.C. Rich), a member of the Bignoniaceae family. Young (1974) found that whereas freshly eclosed females and males both fed on fruit in the afternoon, older females tended to feed in the morning and afternoon. DeVries (1987) also reported that males and females are active at different times in the day and occupy different microhabitats, with males tending to follow rivers and forest edges whereas females are less conspicuous and tend to be found only in the forest. No significant difference in horizontal distribution pattern between the *Morpho peleides* sexes was found from the

data in this study (G=5.46, df=2, p>0.05). Young (1974) also reports a bias in the sex ratio of more males to females (1.86: 1), attributing this to the fact that females are more cryptic in their behaviour and so encountered less frequently. However, a similar sex ratio of males to females of approximately 2:1 was found in study 1 (1.94: 1) and study 2 (2.17: 1), therefore excluding crypsis as a possible explanation of the sex ratio bias.

No significant differences between ratios of recapture events within forest blocks against recapture events within plus those leaving and entering forest blocks was found when the recapture events of all species were compared, but there was a significantly lower ratio of recapture events between traps within the northernmost block compared with other blocks when only *C. penelope* recapture events were analysed. If this ratio is taken as a measure of residency, then low residency was seen in this northern block of forest compared with the strip or the southern block of forest for *C. penelope*. This is consistent with the finding that *C. penelope* individuals are found in greater abundance at north-facing edges which were both present in the strip and southern blocks but not in the northern block.

The movement patterns of *C. penelope* and *Morpho peleides* individuals were found to be significantly different in terms of the relative distances flown by the individuals of these two species. Relatively more *C. penelope* recapture events were recorded between shorter distances, compared with a more even spread of distances flown for *Morpho peleides*. This is likely to reflect the greater flight capabilities of the larger-winged *Morpho peleides*, and may imply a larger home-range for this species.

The movement across breaks between forest blocks observed for individuals of five species, was not found to be significantly different from the number of individuals expected to cross, using the formula derived by Munguira and Thomas (1992). The seven other species recaptured crossing breaks were not tested for significance due to expected values of less than five. For those species which were recaptured but not recorded crossing breaks, none generated expected values ≥ 5, and so were not tested

have been seen either crossing breaks (*Hamadryas feronia*, *C. libye*, *Archaeoprepona* or *Prepona* species), flying in one of the breaks (*Biblis hyperia*, *Adelpha* species), or feeding in open areas (*Opsiphanes cassina*, *Historis acheronta*). Further sampling would increase the probability of recapturing individuals of these species crossing the breaks. Munguira and Thomas (1992) found that wide busy roads were no barrier to the movements of temperate species living in open populations, but slightly impeded those with closed populations. Although Adonis blue butterflies *Lysandra bellargus* were found to readily fly 250 m over open calcareous grassland, they appeared not to do so over 100 m gaps of agriculturally improved grass, hedge and scrub (Thomas 1983). Similarly, Warren (1987a,b) found that the heath fritillary *Mellicta athalia* moved along woodland rides between clearings within continuous patches of woodland, but almost never across even short stretches of farmland from one isolated wood patch to another. Male euglossine bees have been found unable to cross 100 m breaks of open ground between forest patches in Amazonia (Powell and Powell 1987).

Field observations on birds support the hypothesis that some forest species avoid crossing open areas (Martin and Karr 1986, Opdam *et al.* 1985, van Dorp and Opdam 1987, Willis 1974, Yahner 1983), and the same has been found for forest-dwelling mice (*Apodemus flavicollis*) and carabid beetles (Mader 1984).

It is realised that the movements described in this study are entirely dependent on the positioning of the fruit traps and that the number and spacing of these traps are a limiting factor. A larger grid may well uncover the more subtle differences in the extent of movements between species. This study has shown that with a simple and small grid of fruit traps (relative to the size of forest habitat), horizontal stratification at a forest edge and the propensity of species to cross forest breaks can be addressed. The movements described are also those of individuals foraging for food. It is not known how these movements reflect daily or seasonal movements with respect to other adult resources such as mates or larval hostplants.

Chapter 5

Fruit-feeding butterflies in different aged gaps and non-gaps in selectively logged forest

5.1. Introduction

The fruit-feeding butterflies of three selectively logged forest habitats were sampled using fruit traps in gaps and adjacent non-gaps. These three forest habitats differed in the period of time since logging and a 'gap' represented a site where a tree had been selectively felled and a gap in the canopy had originally existed, although not neccessarily at the time of sampling.

The composition of butterfly assemblages in disturbed and undisturbed forest habitats (Ch.3) and the effects of thin breaks between forest blocks to butterfly movement patterns have been explored (Ch.4). The scale of study is refined further in this Chapter to examine the fruit-feeding butterflies in gaps created by selective removal of individual trees, compared with non-gaps in the same forest habitats, after different periods of recovery time. The sampling was undertaken in the Periodic Block System of management (Ch. 2). Each habitat (block) was described by the length of time since it had been logged and associated vegetation characteristics such as basal area per hectare, tree density and stand structure.

The direct result of a treefall is a gap in the forest and an area of affected vegetation (Ch.1). The gaps studied here were all likely to have been relatively small initially, caused by the removal of single tree crowns from the canopy in most cases. In terms of research into the effects of gap formation and closure on the forest's fauna is concerned, little information is available. Work on birds in Malaysia (Wells 1988), however, found that two gaps of 0.5-1 ha extent took about ten years to acquire their

first true shade-adapted birds. This avoidance of pioneer growth by these birds was thought to be due to sensitivity to high temperatures and a well known behavioural avoidance of bright light.

I believe this study represents the first to look at any invertebrate group in the context of tropical forest gaps and their subsequent closure. Data concerning the effects of selective logging upon insect faunas have been reported as lacking (Sutton and Collins 1991).

The main objectives of the work described in this Chapter are:

1) to characterise each forest block in terms of vegetation structure using a point-centred quadrat approach, and the % canopy openness of the forest canopy at each fruit trap site through the analysis of hemispherical photographs.

2) to investigate the fruit-feeding butterfly assemblages of gaps and non-gaps in three forest habitats which had been selectively logged in the year of the study (0-year), 5 and 30 years previously.

3) to look at the relationship of canopy openness and species abundance in terms of the progression of time since logging.

5.2. Methods

This study was carried out in three blocks of the Periodic Block System (PBS) (Ch. 2) in the Victoria-Mayaro forest reserve (Fig. 2.1). Block 1 (B1) had been logged 5 years previously (and 30 years before that) and B6, with logs being extracted at the time of sampling (and 30 years previously), referred to as 0 years ago, were situated opposite each other, separated by a road. B7 had been logged 30 years previously and was the next block to be opened for logging. B7 was on the same side of the road as B6, about 1.5 km away, separated by 500 acres (202 hectares) of B2. Vegetation sampling included a primary forest habitat for comparison from within the Victoria Mayaro reserve. This area of primary forest was studied in 1994 (Ch.4) and is in the same area as a Forestry Division Permanent Sample Plot (PSP80).

5.2.1. Habitat structure

A measure of the habitat structure of the three blocks and a primary forest site, in terms of tree size class structure, basal area and tree density, were made using the point-centred quarter method (Cottam and Curtis 1956, Curtis and McIntosh 1950, Stearns 1949). First, a compass bearing was chosen which traversed the habitat in the same area that the butterfly sampling was undertaken. Along this compass bearing, 50 x-y co-ordinates were found, using a selection of randomising methods which are described in the next paragraph, at which the closest tree in each of the four quarters were used to sample the habitat's vegetation structure.

Random numbers between 0 and 100 were looked up in random number tables, and these became the sequential number of paces which were walked along the compass bearing. Having paced out the first random number between 0 and 100, a coin was flipped to decide whether to proceed to the left or right and then a 50 m measuring tape was laid out. Five random numbers between 0 and 10 then decided sequential distances along the tape. At each of these distances a coin was flipped to determine left or right,

and another random number between 0 and 10 decided the number of paces to the sampling point. Once these five points (20 trees) had been sampled along the 50 m tape, the tape was reeled in to the original compass bearing line, and the next random number between 1 and 100 along the compass bearing paced out. This was repeated another nine times.

Each randomly chosen sampling point (x-y co-ordinate) was considered the centre of four quarters, orientation of which was given by the direction of the transect line. The closest tree in each of these four quarters were, collectively, the sample of four trees at this randomly chosen x-y co-ordinate.

The distance to each tree, from this randomly chosen point, and the dbh of each tree were measured. Only trees with a diameter at breast height (dbh) greater than 10 cm were included. 50 of these randomly chosen points were selected in each habitat, a total of 200 trees. The average of the four distances at each sampling point is equal to the square root of the mean area, as demonstrated empirically by Cottam *et al.* (1953) and theoretically by Morisita (1954). Hence each habitat produced 50 mean areas from which an overall mean area was produced. This method has the major advantage over standard plot techniques, in being much more efficient in terms of results per person-hour expended. Cottam and Curtis (1956) compared four sampling methods which utilize spacing distances with the fixed-area plot method. They sampled the vegetation of three forest communities and an artifical random population using these five methods - the closest individual, the nearest neighbour, the random pairs, the point centred quarter and the quadrat. They found that all the distance methods were capable of producing accurate results when an adequate sample was used, but the size of an adequate sample varied with the method. The point-centred quarter method gave the least variable results for distance determinations and was found to be the least susceptible to subjective bias. The disadvantage of requiring more time to sample each point is compensated for by the necessity for sampling fewer points.

5.2.2. Hemispherical photographs of the forest canopy

Hemispherical photographs of the forest canopy were taken at each fruit trap site (four gaps and four non-gaps in each block), to obtain a measure of canopy openness (Anderson 1964). This technique has been used to determine canopy openness in both tropical (Raaimakers *et al.* 1995, Rich *et al.* 1993, Smith *et al.* 1992, Whitmore *et al.* 1993) and temperate forests (Easter and Spies 1994, Valverde and Silvertown 1995, Walter and Himmler 1996), and to characterise the overwintering sites of Monarch butterflies *Danaus plexippus,* in Mexico with respect to canopy cover (Weiss *et al.* 1991).

The camera was set on a tripod 50 cm above ground level, with the lens pointing vertically at the forest canopy, a spirit level used to ensure that the camera body was horizontal, and the top of the camera pointing north. Photographs were taken with an Olympus Auto-fisheye lens (1:2.8, f=8mm) using a black and white, high contrast film (Ilford PANF, ASA 125). Two photographs were taken at each location with exposure settings of f5.6, f8 and occasionally f11 when photographing a large gap. Photographs were taken in the early morning to take advantage of optimum brightness light conditions, whilst avoiding over exposure from the sun located directly overhead. This would create excessive glare on photographs, concealing the subtleties of vegetation and non-vegetation.

The computer program Image 1.42 (Macintosh) was used to capture the hemispherical images of the negatives on a light table, through a JVC TK-5310 video camera. Contrast and brightness of the captured image were adjusted over all of the image by comparing with the contact prints. In certain cases, drawing tools were used to modify the image for clarity, eg. to emphasize the distinction between dark cloud and vegetation. This procedure may introduce errors but human interpretation is preferable to arbitrary standards, as these differences can sometimes be too subtle for the resolution of the computer (Chazdon and Field 1987).

These images were then converted into MacDraw images in which closed canopy areas were black and open areas were white (a one-bit screen map). These standardized images were then analysed quantitatively using the software program Solarcalc 5.41 (Macintosh II), developed by Chazdon and Field (1987). The key parameter obtained from this analysis was diffuse light, measured as the percentage of open sky in the hemispherical photograph (Anderson 1964, Mitchell and Whitmore 1993).

5.2.3. Butterfly sampling

Fruit-feeding butterflies were sampled in each block using fruit trapping and mark-release-recapture techniques (Ch. 2). Within each block, a fruit trap was placed in each of four gaps (as close to the centre as possible) created by the removal of a tree (cut tree stumps being characteristically different from tree stumps left from natural tree falls), so that each gap was known to be either 0, 5 or 30 years old depending on the block. Fruit traps were also placed in four non-gaps in each of these blocks. The fruit traps were baited and checked every afternoon between 15.00 and 17.30 pm.

Species capture data were used to examine species' preferences for gaps and non-gaps in the different forest blocks. Movements between gaps and non-gaps were investigated by looking at the number of recapture events in each forest block that occurred from a) gap to gap, b) non-gap to non-gap, c) gap to non-gap and d) non-gap to gap. Differences in the ratios from 1: 1: 1: 1 were tested for significance using the G-test.

The effects of forest block, or time since logging (0, 5 and 30 years), and the effect of gap (four replicates) or non-gap (four replicates) on several butterfly variables, were tested for statistical significance using a two-way ANOVA with replication. This was undertaken for the following butterfly variables; number of species, number of new individuals of all species, number of recaptured individuals of all species and number

of new plus recaptured individuals of all species. It was also carried out for numbers of new individuals of those species found in sufficient abundance (> 50 % of gap or non-gap sites with captures), in this case *Cissia arnaea* and *Colobura dirce* (Plate 5.1). Post-hoc (Tukey HSD) tests were also carried out.

5.3. Results

5.3.1. Habitat structure

For the 0-year (B6), 30-year (B7) and primary habitats, point-centred quadrats revealed that overall basal area values were greater with increased length of time since logging. B1, logged 5 years previously, was unusual however, having the highest basal area of all habitats sampled (Table 5.1), although none of these differences were significant (B1&P, G=0.513, df=1, p>0.05; B1&B7, G=0.638, df=1, p>0.05; B1&B6, G=2.43, df=1, p>0.05). The 5-year forest appeared to be different from the other forest habitats in that it was covered in standing water in areas that appeared more permanent than seasonal.

Table 5.1. Summary of results from the point-centred quadrat survey in each block and a primary forest comparison.

	0 yrs (B6)	5 yrs (B1)	30 yrs (B7)	Primary
Sample basal area (total)	12.81	22.09	15.04	19.79
Basal area (mean)	0.06	0.11	0.08	0.10
Total distance	988	1070	970	1102
Mean distance per stem	4.97	5.35	4.88	5.51
Density of stems ha^{-1}	405	349	424	329
% *Mora* stems ha^{-1}	67.0	64.8	74.4	21.9
Basal area (total) m^2ha^{-1}	26.1	38.6	31.9	32.56

Distributions of stem dbh class sizes revealed that primary forest had more stems in the smallest (10-19 cm) and largest (>100 cm) dbh classes than any of the blocks (Table 5.2.a and Fig. 5.1) and 0-year forest had the fewest stems in the six largest dbh class sizes. Significant differences in stem distributions between size classes were found between the 0-year forest and all other forest comparisons (primary, G=18.77, df=5, p<0.01; 30-year forest B7, G=14.85, df=5, p<0.05 and 5-year B1, G=15.25, df=5, p<0.01). A significant difference was also found between the primary and 5-year forest (G=13.8, df=6, p<0.05) but not the 30 and 5-year forest (G=10.17, df=6,

p>0.05). No significant difference was found either between the primary and 30-year forest distributions (G=3.97, df=6, p>0.05).

Table 5.2.a. Proportion of 200 stems in each size class of trees with dbh ≥10 cm, from sets of 50 point-centred quadrats in Trinidad primary forest and three forest blocks under PBS management. See Figure 5.1.

Dbh size class (cm)	0-year (B6)	5-year (B1)	30-year (B7)	Primary forest
10-19	0.390	0.335	0.495	0.505
20-29	0.285	0.255	0.200	0.215
30-39	0.195	0.155	0.110	0.100
40-49	0.055	0.060	0.060	0.030
50-59	0.035	0.070	0.055	0.065
60-69	0.025	0.060	0.050	0.035
70-79	0.005	0.040	0.025	0.010
80-89	0.005	0.010	0	0.010
90-99	0	0.005	0.005	0.010
≥100	0	0.010	0	0.020

The proportion of stems in the 20-29 and 30-39 cm dbh size classes revealed a predictable sequential pattern with age since logging (Table 5.2.b), with significantly more stems in these size classes in the 0-year than either the 30-year or primary forest (Table 5.2.c for G-test values and significance of comparison). The size class distributions of trees from the primary forest (using point-centred quadrats in 1996 and 20 x 10 m quadrats in 1994) were compared with distributions from other tropical primary forests (Table 5.3).

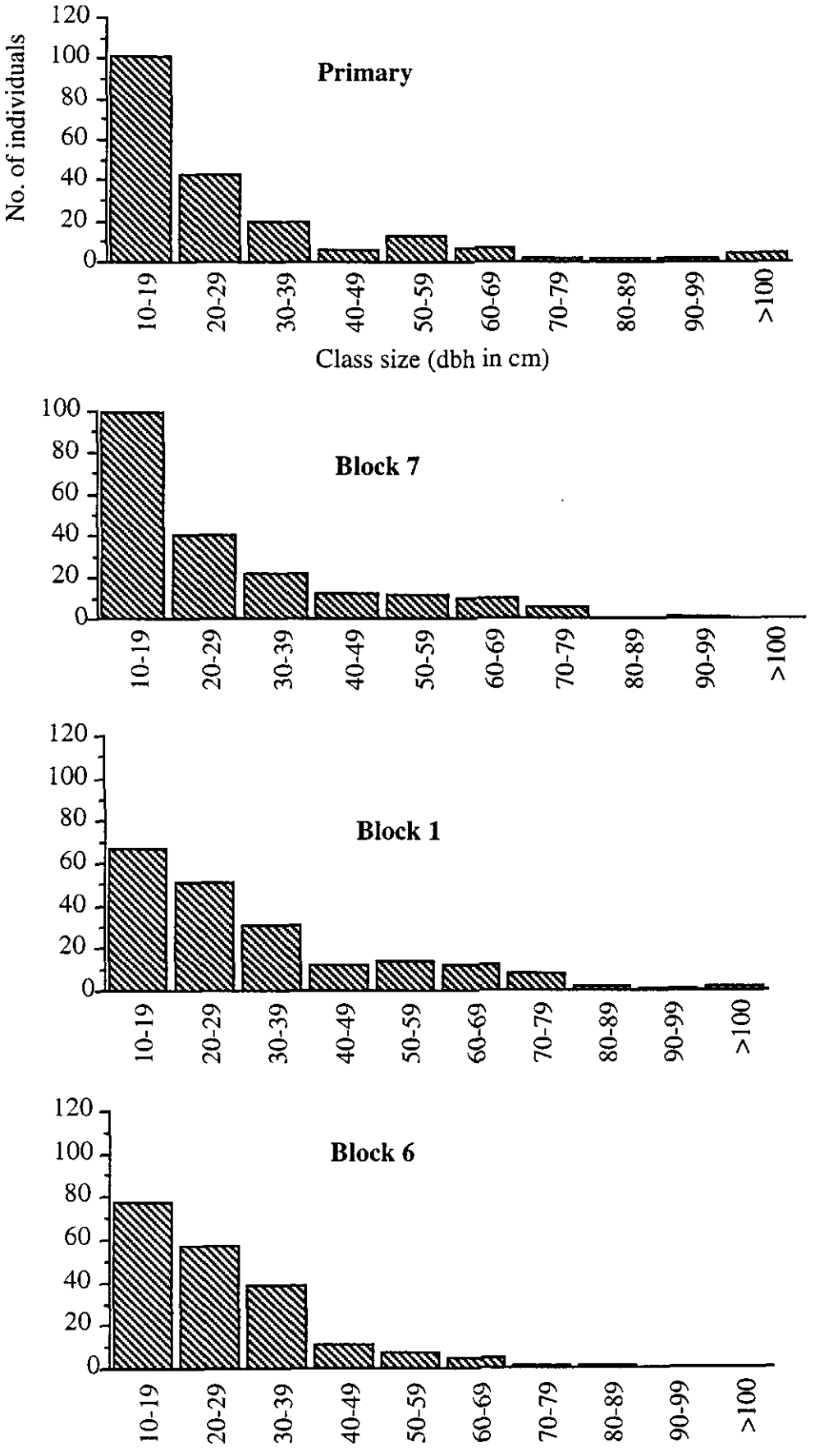


Figure 5.1. Size class distribution of trees with dbh ≥10 cm in Trinidad primary forest compared with the same PBS forest 0 years (B6), 5 years (B1) and 30 years (B7) after logging

Table 5.2.b. Number of stems in the 20-29 and 30-39 cm dbh size classes with dbh ≥10 cm, from sets of 50 point-centred quadrats in Trinidad primary forest and three forest blocks (PBS managed).

Dbh size class (cm)	0-year (B6)	5-year (B1)	30-year (B7)	Primary forest
20-29	57	51	40	43
30-39	39	31	22	20
TOTAL	96	82	62	63

Table 5.2.c. Statistical comparison of numbers of stems in the 20-29 and 30-39 dbh size classes. G-values shown, all tests had df=1, N.S.: no significance.

	5-year	30-year	primary
0-year	1.25, N.S.	7.8, p<0.01	8.2, p<0.01
5-year	-	2.87, N.S.	3.073, N.S.
30-year	-	-	0.2, N.S

Table 5.3. Proportion of stems in each size class of trees with dbh ≥10 cm in Trinidad primary forest using two sampling methods, compared with other primary tropical forests where size class distributions were available. Data from: **1.** Swaine, M.D. *et al.* (1984); **2.** Gentry & Terborgh (1990); **3.** Rankin-de-Merona *et a* (1990) and **4.** Manokaran & Kochummen (1984).

Dbh size class (cm)	Trinidad 1994	Trinidad 1996	Kade Ghana (1)	Cocha Cashu Peru (2)	Amazonas Brazil (3)	Sungei Menlaya (4)
10-19	0.516	0.505	0.635	0.632	0.657	0.611
20-29	0.262	0.215	0.200	0.205	0.196	0.191
30-39	0.095	0.100	0.074	0.092	0.078	0.086
40-49	0.040	0.030	0.037	0.019	0.032	0.049
50-59	0.024	0.065	0.019	0.015	0.018	0.022
60-69	0.008	0.035	0.013	0.012	0.009	0.014
70-79	0.016	0.010	0.004	0.010	0.005	0.011
80-89	0.016	0.010	0.006	0.006	0.003	0.008
90-99	0.016	0.010	0.002	0.002	0.001	} 0.009
≥100	0.008	0.020	0.011	0.007	0.001	
Basal area (m^2ha^{-1})	56.6	32.6	30.85		30.6	32.4
Tree density (stems ha^{-1})	620	329	552		647	492

5.3.2. Hemispherical photographs of the forest canopy

Canopy openness values were arcsine transformed, the standard procedure for transforming values expressed as percentages or proportions (Sokal and Rohlf 1981). Significant effects of block (two-way ANOVA, F=20.7, df=2, p=0.00002), gap - non-gap (two-way ANOVA, F=4.58, df=1, p=0.046) and the interaction between these factors (two-way ANOVA, F=5.64, df=2, p=0.0126) were found on transformed canopy openness values. Tukey HSD post-hoc tests revealed that the 0-year gaps were significantly more open than the non-gaps (p=0.0099), 5-year gaps (p=0.0002) and non-gaps (p=0.0003), and 30-year gaps (p=0.0004) and non-gaps (p=0.0004). All other comparisons were non-significant. The mean percentage canopy openness values are shown in Figure 5.2 and Table 5.4.

Figure 5.2. Mean % canopy openness values for gaps (four) and non-gaps (four) from analysis of hemispherical photographs.

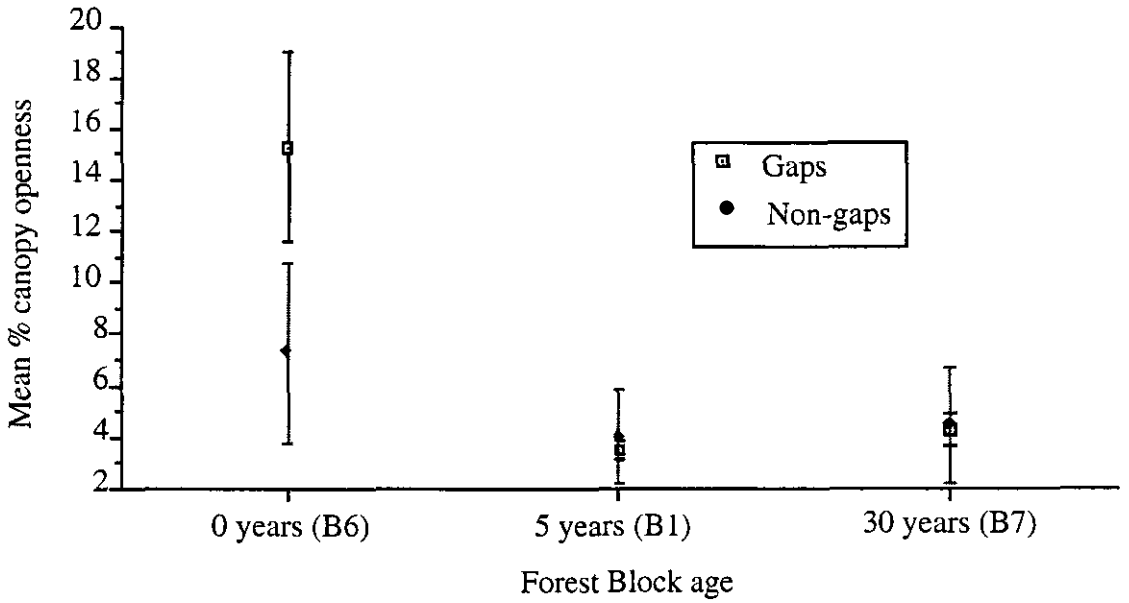


Table 5.4. Mean % canopy openness values for hemispherical photographs for four gaps, four non-gaps and a combination of both (eight) in 0-year, 5-year and 30-year forest.

	0-year			5-year			30-year		
	Gaps	**Non**	**Both**	**Gaps**	**Non**	**Both**	**Gaps**	**Non**	**Both**
Mean % canopy openness	15.29	7.30	11.29	3.50	3.98	3.74	4.32	4.47	4.39
S.d.	3.70	3.51	5.42	0.38	1.78	1.22	0.58	2.25	1.53

5.3.3. Butterfly sampling

A total of 21 species (species group in the case of *Caligo* species) and 287 new captures were encountered in this study. The two most abundant species encountered in this study were *Colobura dirce* and *Cissia arnaea* comprising 30 and 26 % respectively of all new captures. The number of new captures of each butterfly species in gaps and non-gaps in each forest block are shown in Appendix B.2.

When the total recapture events in each block from gap to gap, non-gap to non-gap and gap to non-gap (Tables 5.5.a and 5.5.b) were analysed with respect to a 1: 1: 1: 1 ratio, it was found that for both the 0-year and 5-year forests, the number of expected recapture events in each category was less than five. Therefore, recapture events were analysed under the hypothesis that there was no difference between the number of recapture events between the same microhabitats (i.e. gap and gap, and non-gap and non-gap) and opposite microhabitats (i.e. gap and non-gap, and non-gap and gap). A significant difference from a 1: 1 ratio was found for the recapture events in the 0-year forest (B6, $G=17.23$, $df=1$, $p<0.001$) but not in the 5-year (B1, $G=0.06$, $df=1$, $p>0.05$) or 30-year forest (B7, $G=0.125$, $df=1$, $p>0.05$).

Table 5.5.a. Total recapture events for all species in this study, recorded between gap and gap, non-gap and non-gap, gap and non-gap and non-gap and gap.

	Gap and gap	Non-gap and non-gap	Gap and non-gap	Non-gap and gap
0-year (B6)	15	3	0	1
5-year (B1)	5	4	3	5
30-year (B7)	12	5	7	8

Table 5.5.b. The number of species movements (recapture events) between gap and gap, non-gap and non-gap, gap and non-gap and non-gap and gap, in each of the three blocks studied (in bold in parentheses)

Species	Total captures (gaps plus non-gaps)	Gap and gap	Non-gap and non-gap	Gap and non	Non-gap and gap
Cissia arnaea	4(**6**);16(**1**);54(**7**)	12(**7**)	1(**6**);3(**1**);3(**7**)	1(**1**);7(**7**)	2(**1**);6(**7**)
C. hesione	7(**6**);3(**1**);0(**7**)	1(**6**)			
C. myncea	3(**6**);2(**1**);1(**7**)		1(**6**)		
C. penelope	18(**6**);7(**1**);1(**7**)	6(**6**)			
Caligo species	4(**6**);11(**1**);7(**7**)	2(**1**)	1(**1**);1(**6**)	1(**1**)	
Catoblepia berecynthia	1(**6**);4(**1**);2(**7**)				1(**6**);1(**1**)
Colobura dirce	40(**6**);33(**1**);15(**7**)	8(**6**);3(**1**)		1(**1**)	2(**1**);1(**7**)
Morpho peleides	1(**6**);1(**1**);5(**7**)		1(**7**)		1(**7**)
Taygetis cleopatra	1(**6**);0(**1**);6(**7**)		1(**7**)		

Two-way analysis of variance with replication on the total number of species encountered, revealed no significant effect of age since logging ($F=0.093$, $df=2$, $p=0.912$) or of gap or non-gap ($F=1.49$, $df=1$, $p=0.24$). Significantly more new individuals of all species ($F=4.77$, $df=1$, $p=0.0424$) and new plus recaptured individuals of all species ($F=4.73$, $df=1$, $p=0.043$) were found in gaps than non-gaps but no effect of age since logging was found ($F=0.297$, $df=2$, $p=0.747$ and $F=0.545$, $df=2$, $p=0.589$, respectively). No significant effect of either factor was found for the total number of recaptured individuals of all species (age since logging, $F=1.17$, $df=2$, $p=0.33$; gap or non-gap, $F=3.29$, $df=1$, $p=0.086$).

The number of *Cissia arnaea* new captures data were log transformed, making the variances homogeneous and the errors normally distributed. A significant effect was found of age since logging (two-way ANOVA with replication, F=19.23, df=2, p=0.000034). No significant effect of gap - non-gap (F=0.765, df=1, p=0.393) or interaction between the two factors were found (F=2.092, df=2, p=0.152). Post-hoc tests (Tukey HSD) showed significantly more new *C. arnaea* individuals were caught in 30-year forest gaps than 0-year gaps (p=0.00034) and non-gaps (p=0.00114), and 1-year gaps (p=0.0387) and non-gaps (p=0.0258). No significant difference was found between 30-year gaps and non-gaps (p=0.34). Significantly more *C. arnaea* individuals were also present in 30-year non-gaps than 0-year gaps (p=0.0166). All other comparisons were non-significant.

When a two-way ANOVA was carried out on the *Colobura dirce* data, which did have a homogeneous variance and normally distributed errors, no significant effect of age since logging (F=3.13, df=2, p=0.068), gap - non-gap (F=0.904, df=1, p=0.354) or of the interaction was found (F=1.37, df=2, p=0.278). The *C. arnaea* and *Colobura dirce* new captures data are illustrated graphically with respect to mean % canopy openness values (Fig. 5.3.a and b).

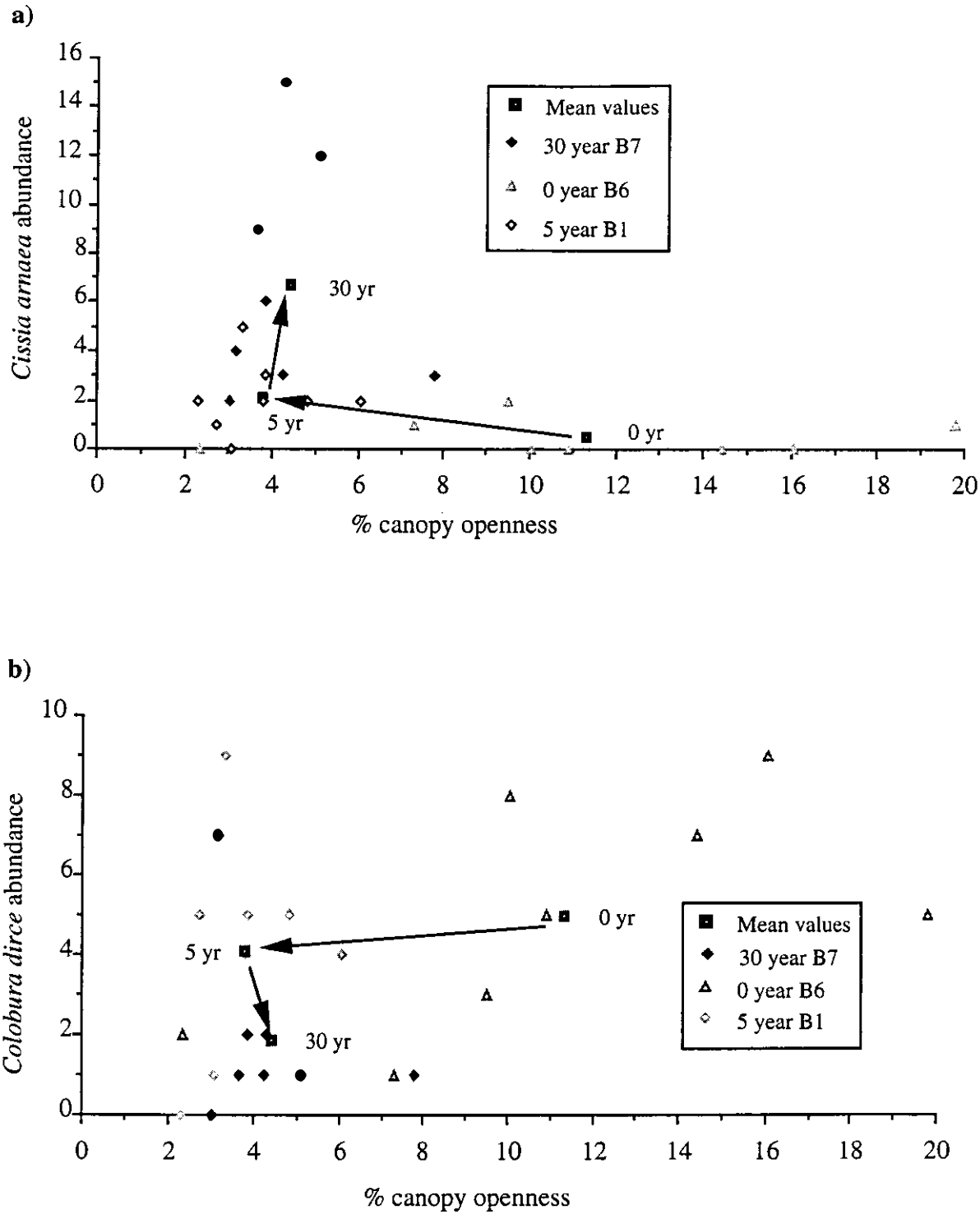


Figure 5.3. The abundance of a) *Cissia arnaea* and b) *Colobura dirce* against % canopy openness from hemispherical photographs. Mean abundance and % canopy openness values are shown and arrows indicate the progression from 0 to 5 to 30 years after logging.

Plate 5.1. *Colobura dirce* larvae feeding on *Cecropia peltata* (left) and an adult *Colobura dirce* feeding on mango (right)

5.4. Discussion

Under the PBS of selective logging in Trinidad, an area logged 30 years previously (B7) was seen to have a distribution of stems in class sizes not significantly different from primary forest. Significant differences in the smaller size classes were found immediately following logging (B6) and five years after logging (B1), compared with primary forest and forest 30 years after logging (B7). In both primary and 30-year forest there were found to be more than double the number of stems in the 10-19 cm dbh class size compared with the 20-29 cm class size (ratios of 2.4: 1 and 2.5: 1 in each habitat respectively). In both 0 and 5-year forest this ratio was 1.3 in both habitats, with the number of stems in the 10-19 cm class decreasing and the number in the 20-29 cm class size increasing relatively. In all of the other tropical primary forest habitats cited (Table 5.3), this ratio was found to be greater than three (between 3.1 and 3.4). The number of stems in these smaller class sizes are indicative of the recruitment rates of these forest habitats. Many of the stems in the smaller size classes in the recently logged habitats are likely to have been lost during the logging and extraction process.

The total basal area value of 32.6 m^2ha^{-1} (stems ≥ 10 cm dbh) for the primary forest habitat in Trinidad compares well with the value obtained by Beard for virgin *Mora* forest in Trinidad of 38 m^2ha^{-1} (Beard 1946) and with basal areas of other tropical primary forest habitats (between 30.6 and 32.4 m^2ha^{-1}) where data on stem class size distribution were also available (Table 5.3). A greater basal area of 56.6 m^2ha^{-1} (stems ≥ 10 cm dbh) was obtained for the same primary forest habitat in 1994 from ten 20 x 10 m quadrats (Ch.3). This difference in basal area estimates from the same habitat may be due to differences in sampling methods. Selective logging in a forest block generally reduced the total basal area of tree stems compared with that found in primary forest, as might be expected, apart from the 5-year forest which had the highest total basal area. No significant differences in basal areas were found between the blocks, however, and no knowledge of pre-logging basal areas or the relative volumes (basal

areas) of wood extracted from each block, is known either. What was also found was that the three blocks were dominated by *Mora excelsa* (65-74 % of stems), whereas in the primary forest, *Mora excelsa* constituted only 22 % of stems. The slight undulating topography of the primary forest habitat relative to the blocks may be the reason for this, with *Pentaclethra macroloba* dominating the ridges. The use of the primary forest as baseline unlogged *Mora* forest against which the effects of logging and subsequent length of recovery were compared, therefore, was carried out with these reservations in mind.

The canopy above gaps in the 0-year forest was significantly more open than the gaps in the 5 and 30-year forests, and the non-gaps in all three blocks. It was apparent that 5 years after logging, gaps had closed to levels not significantly different from non-gaps or gaps 30 years after logging. A similar result was found in a study in Venezuela where mean values of percentage canopy openness were significantly lower in primary forest than forest logged less than a year previously (5.9 $\pm$ 1.5 and 28.1 $\pm$ 25.6 respectively), but were not significantly different in forest logged 5-6 years earlier (9.1 $\pm$ 7.3) (Mason 1996).

In the 0-year forest, significantly more recapture events were recorded between the same microhabitats (gap to gap and non-gap to non-gap) than between opposite microhabitats (gap to non-gap and non-gap to gap). No significant difference from a 1: 1 ratio was found in the other blocks. It was also only in 0-year forest where a significant difference in mean % canopy openness value existed between gaps and non-gaps, whereas when no significant difference in canopy openness existed between gaps and non-gaps (5 and 30-year forests), no significant difference from a 1: 1 ratio of number of recapture events was found. This appears to show that species may be choosing to feed in specific microhabitat conditions, i.e. in either more open or more closed canopied forest areas, and not feeding in both, when these two microhabitat conditions are distinguishable in terms of canopy openness.

Overall, no significant effect of whether a fruit trap was situated in a gap or a non-gap or age since logging, was found for the number of butterfly species captured. Significantly more individuals, however, were captured in gaps rather than non-gaps, with no effect of the time since logging. Workers in montane forest in northern Vietnam found that butterfly species richness and diversity was higher in gaps than non-gaps (Spitzer *et al.* 1997), with the gap species being mostly more opportunistic butterfly species with wider geographic ranges. Work in forest fragments in Manaus, Brazil, also showed a dramatic increase in butterfly species richness in forest habitats with increased light levels in the understorey, such as in large internal clearings and fragments which were semi-isolated (increased proportion of edge habitat), compared with inside forest (Brown 1991, Lovejoy *et al.* 1986). Another example of greater species richness being found in gaps is given by Sparrow (1994) where a road transect in Costa Rica, following a wide, continuous light-gap, produced 74 % more butterfly species than a trail transect that traversed undisturbed forest with scattered light gaps.

The two species, *Cissia arnaea* and *Colobura dirce*, revealed contrasting differences in mean abundance with respect to mean % canopy openness in the three blocks and time since logging. *C. arnaea* abundance was lowest in the 0 and 5-year forest and significantly more abundant in the 30-year forest. This result suggests that forest with high mean % canopy openness is unsuitable habitat for *C. arnaea*. A forest canopy with a lower mean % canopy openness is still not suitable after 5 years, but is after some period of between 5 and 30 years after logging. *C. arnaea* is a hostplant specialist, the larvae feeding solely on one species of grass, *Ichnanthus pallens* (Poaceae) (Singer and Ehrlich 1993). Two other species of butterfly in the *Cissia* group (*C. junia* and *C. erichto*) are also hostplant specialists, compared with nine *Cissia* species which have all found 13 species of grass and sedge acceptable (Singer and Ehrlich 1993). All specimens of *I. pallens* in the UWI Herbarium in Trinidad, have been collected from shaded forest tracks, open areas in primary forest and stream banks (Johnston and Oatham, *pers. comm.*). It is suggested here that perhaps disturbance and opening of the forest canopy create microhabitat conditions that are

immediately unsuitable for *Ichnanthus pallens* and only after a period of time between 5 and 30 years later, are conditions suitable for the re-establishment of *I. pallens* and subsequently *C. arnaea*.

A contrasting pattern of butterfly abundance and mean % canopy openness was found for *Colobura dirce* in the three blocks, although none of these differences were significant. *Colobura dirce* was found in greatest numbers in the 0 and 5-year forest and lowest in the 30-year forest. *Colobura dirce* appears to be found in more recently disturbed forest. It is only at some point in time between 5 and 30 years after logging that *Colobura dirce* abundance declines. *Colobura dirce* is also a hostplant specialist, the larvae feeding on *Cecropia peltata* (Plate 5.1), a pioneer tree species that dominates disturbed forest habitats such as forest edges and gaps. The disturbance caused by logging and extraction are ideal for the establishment of *Cecropia peltata*, and hence perhaps for maintaining populations of *Colobura dirce*. As forest recovery progresses following logging, succession will lead to the pioneer *Cecropia peltata* species being out-competed by primary tree species, and consequently the number of hostplants and inevitably the suitability of the forest habitat for *Colobura dirce*.

So whereas few *C. arnaea* individuals were encountered following selective logging, until between 5 and 30 years later, more *Colobura dirce* individuals were found following logging up to 5 years later and fewer individuals between 5 and 30 years later. It would be interesting to discover whether the switch from high to low abundance in these two species, occurred at the same point in forest recovery after logging.

Chapter 6

Residency, longevity, population size and the effects of the MRR procedure

6.1. Introduction

This Chapter investigates the residency and population size of the more abundant species encountered in the MRR studies of Chapter 4.

The average length of time individuals of a species spend in a study area is referred to as the average 'residency' time (Ehrlich 1961), as the cause of loss from a population is indistinguishable between death and emigration. The longest individual residency times recorded, for several species, are given as an indication of potential longevities of these fruit-feeding species. Residency times and half-day (either morning or afternoon) population estimates, with confidence limits, are derived for *Cissia penelope* and *Morpho peleides* over the duration of study 1 and study 2 (see Ch. 4), and a total population size of both species, over the duration of both studies, estimated. Half-day population size estimates are derived for *Colobura dirce*, *Cissia hermes* and *Taygetis andromeda.*

Chapter 4 investigated the horizontal stratification of fruit-feeding species relative to a forest edge (study 1; sites 1 and 2) and the movement patterns across breaks in the forest (study 2). This Chapter uses the MRR data from these two studies to calculate the population parameters mentioned above.

The sizes of adult butterfly populations have been estimated in temperate (Brakefield 1982, Dowdeswell *et al.* 1940, Munguira and Thomas 1992, Warren 1987a, Watt *et al.* 1977) and tropical habitats (Cook *et al.* 1976, Ehrlich and Gilbert 1973, Emmel 1970, Turner 1971). The flight period of many temperate butterflies last relatively short,

discrete periods of time, often four to six weeks in a year (see (Thomas and Lewington 1991) for examples), and hence populations can be monitored over their entire flight period relatively easily. Another feature of many temperate species is their propensity to remain within the vicinity of their larval host-plant, for the duration of their life, with little emigration (e.g. *Plebejus argus* Silver-studded blue, *Hesperia comma* Silver-spotted skipper, *Thymelicus acteon* Lulworth skipper and *Mellicta athalia* Heath fritillary), (Thomas *et al.* 1992). About 80 % of British species are thought to form closed populations, and the great majority have been known to survive in very small areas of less than two hectares (Warren 1992). By choosing the size of the study area to encapsulate the discrete patches of larval-hostplant habitat, and knowing that little dispersal occurs between habitat patches, these populations are effectively 'closed'.

In tropical forests, adult butterflies are present throughout the year, in greatest abundance following the onset of the wet season and decreasing over the course of the dry season. At any one moment in time, these populations may comprise individuals from several over-lapping generations. From the number of *Cissia penelope* and *Morpho peleides* individuals recaptured moving between the two sites set 500 m apart in study 1, and the movements observed across the breaks in study 2 (Ch.4), it was evident that the grids of fruit traps did not encompass all the movements of the *Cissia penelope* and *Morpho peleides* individuals. Migration between study areas was recorded and newly emerged 'fresh' adults often captured. These two species were, therefore, regarded as having 'open' rather than closed populations, at this spatial scale.

The reported effects of handling and marking individuals in MRR studies have ranged from "the marks were inconspicuous and thus were unlikely to affect either the survival of marked individuals or their probability of being recaptured" to the more cautious approach of rejecting data with low recapture rates. MRR studies are often undertaken in order to estimate a population's size. An important premise of the MRR procedure for population size estimation is that marked individuals will mix freely back into the population of individuals from which they were taken, and have an equally likely

chance of being recaught as any other individual in the population, be they marked or unmarked. This premise is often assumed and rarely tested.

The distances flown by individuals upon release after initial capture (when individuals were marked and handled) were compared with those from subsequent captures (just handled). This comparison was used as a method for testing the effect of marking and handling in MRR. Low recapture frequencies are often thought to illustrate the deleterious effect of the MRR technique employed (Morton 1982, Southwood 1978). Another method frequently employed in studies has used the assumption that if the probability of an insect being caught on any sampling occasion remains constant, then the number of successive recaptures, regardless of previous captures, should describe the Poisson distribution for a particular sample size and mean. A significant deviation from the expected values has been thought to indicate a tendency for marked individuals to be recaptured more or less often than expected. It has been put forward, however, that high recapture frequencies and good fits to the Poisson distribution are unreliable indicators of the suitability of a particular MRR technique (Morton 1984). The effect of marking and handling is investigated with these different perspectives in mind.

The mean distance flown upon release by a species was also examined in light of a morphometric component of flight for that species, specifically mean forewing length. Forewing length means and ranges obtained in the course of this study are compared with data from Costa Rica.

The main objectives of the work described in this Chapter are:

1) to generate estimates of population size and average residency time using the MRR data from two fruit trapping studies.

2) to investigate the possible effects of marking and handling in the MRR technique which might affect the probability of an individual being recaptured.

6.2. Methods

The data presented in this Chapter come from studies 1 and 2 described in Chapter 4. This study was carried out in the Trinity Hills Wildlife Sanctuary in the South of Trinidad (Ch. 2) from May 30th to August 26th 1995. The fruit-feeding guild of forest butterflies was investigated by capturing individuals in baited fruit traps (Ch.2). Individual butterflies were each uniquely marked (MRR technique described in Ch.2), enabling individuals to be identified and tracked through time and space. Grids of fruit traps were set up to investigate butterfly movements within forest from a forest edge, study 1, and across thin breaks between forest blocks, study 2. The same data collected in those studies were used in this Chapter to analyse elements of adult population structure.

6.2.1. Estimates of adult population size, residency and longevity

Adult population sizes were estimated for the most abundant species encountered over the course of each study. As explained in the introduction to this Chapter, populations were treated as open populations, as movements had been recorded well in excess of intragrid distances (Ch.4). The movement patterns described were obviously limited by the spatial distribution of the fruit traps. Individuals were lost from and were recruited into the populations throughout the duration of the study period.

In studies 1 and 2 the most abundant species (> 50 new captures in each study) were *Cissia penelope*, *Morpho peleides* and *Colobura dirce*. In study 2 but not study 1, this included *Cissia hermes* and *Taygetis andromeda*. The Jolly-Seber open population method (Jolly 1965, Seber 1982) was used to estimate population sizes for half and whole-days throughout the duration of the studies. In his original paper, Jolly (1965) gave formulae for estimating the variance of population parameters. However, simulation studies (Manly 1971, Roff 1973) have shown that these formulae are not reliable for the direct calculation of confidence intervals for true parameter values. A

more reliable method of calculating the 95 % confidence limits of population size estimates was therefore used (Manly 1984).

Half-days were either morning or afternoon fruit-trapping times. Whole-day data were calculated by combining successive half-day data together. Combining the *C. penelope* site 1 and site 2 data for study 1 (18 fruit traps), allowed a comparison to be made between the population size estimates found in study 1 and study 2 (18 fruit traps) over a similar length of time (23.5 days and 22.5 days respectively), although at different points in the wet season.

The MRR data were initially compiled into Method B tables (Jolly 1965). An example is given here for the half-day data for *C. penelope* in study 2 (Appendix C.1). The variables generated from Method B tables are; m_t (number of marked animals caught in sample t), u_t (number of unmarked animals caught in sample t), n_t (total number of animals caught in sample t, $= m_t + u_t$) and s_t (total number of animals released after sample t = [n_t - accidental deaths or removals]). Two more variables are needed before population sizes can be estimated. These are R_t (the number of the s_t individuals released at sample t and caught again in some later sample) and Z_t (the number of individuals marked *before* sample t, not caught in sample t, but caught at some time after sample t). R_t and Z_t are more easily visualised by looking at a Method B table than from a written description, and so, as an example, $R_{3.0}$ and $Z_{3.0}$ are illustrated in Appendix C.1.

Estimates of population size can then be calculated, following Jolly (1965), from the relationship:

Population size = (Size of marked population) / (Proportion of animals marked)

The proportion of animals marked is estimated as $\alpha_t = (m_t + 1) / (n_t + 1)$, where the + 1 is a correction for bias in small samples (Seber 1982).

The size of the marked population is estimated using the two components of the marked population which exist at any sampling time: (1) marked animals actually caught and (2) marked animals present but not captured at sample *t*. Seber (1982) showed that the sizes of the marked population could be estimated by $M_t = ([(s_t + 1) Z_t] / [R_t + 1]) + m_t$, where M_t = estimated size of the marked population just before sample time *t*. Population size is then estimated from $N_t = M_t / \alpha_t$, where N_t = estimated population size just before sample time *t*.

An example of half-day population size estimation is calculated below using the real values obtained for *C. penelope* in study 2 at sample time 3.0 (the sixth half-day).

From the Method B table (Appendix C.1) it can be seen that:

$m_{3.0}$ (the number of marked animals caught in sample $t_{3.0}$) = 14

$u_{3.0}$ (the number of unmarked animals caught in sample $t_{3.0}$) = 25

$n_{3.0}$ (total number of animals caught in sample $t_{3.0}$ = $m_{3.0} + u_{3.0}$) = 25 + 14 = 39

$s_{3.0}$ (total number of animals released after sample $t_{3.0}$ = [$n_{3.0}$ - accidental deaths or removals]) = 39

$R_{3.0}$ (the number of the $s_{3.0}$ individuals released at sample $t_{3.0}$ and caught again in some later sample) = 27

$Z_{3.0}$ (the number of individuals marked *before* sample $t_{3.0}$, not caught in sample $t_{3.0}$, but caught at some time after sample$t_{3.0}$) = 15.

The proportion of animals marked, $\alpha_{3.0}$ = (14+1) / (39+1) = 0.375.

The estimated size of the marked population, $M_{3.0}$ = ([(39+1) * 15] / [27+1]) + 14 = 35.43.

Therefore, the estimated population size of *C. penelope* in Study 2, $N_{3.0} = M_{3.0} / \alpha_{3.0}$ = 35.43 / 0.375 = 94.48 (Appendix C.2).

Average residency rates were calculated from recapture duration decay plots, following the method of Watt *et al.* (1977) (Watt *et al.* 1977). A recapture duration decay plot is a plot of the natural log of the number of individuals which remained in residence a certain number of days versus that number of days in residence. Hence the first point to be plotted is the natural log of the number of individuals which only remained resident in the study area for one day (in this case the number of individuals which remained resident either of the two half-days comprising this one whole-day), plotted against one day, followed by the natural log of the number of individuals which remained resident for two days and so on, until there are no individuals which remained resident for a number of days (in the case of *C. penelope* in study 2 the gap in the data arose at 25 days). Whole-days (in terms of being resident for one or both of the two half-days which made up the whole-day) were used as this reduced the number of gaps. The data up to the gap in the data were plotted and a regression line fitted. The gradient of this regression is $\ln \phi$, the average residency rate being ϕ. This can then be converted to an average residency time in days $[(-\ln \phi)^{-1}]$ following the methods of Cook, Brower and Croze (1967) (Cook *et al.* 1967). Sufficient data were only available for estimating the residency rates and times for *Cissia penelope* and *Morpho peleides* in studies 1 and 2. For *Cissia penelope*, residency rates and times were estimated for (a) the study 1 data for sites 1 and 2 separately, (b) study 1, site 1 and 2 combined, (c) study 2 and (d) study 1 and 2 data combined. As male and female *C. penelope* were not distinguished in this work, the data are for both sexes together. For *Morpho peleides*, the two sexes were distinguished, therefore residency rates were estimated for (a) females and males separately in study 1 (site 1 and 2 combined) and (b) both sexes pooled. This was also carried out for the data from study 2 and when the study 1 and 2 data were combined.

An estimate of the number of individuals present over the duration of the study was calculated by multiplying the day-specific loss rate by the sum of all the half-day population estimates over the study period (Watt *et al.* 1977). In studies which cover the entire flight period of a species, this value represents the population size of the brood.

The potential longevity of different species was taken from maximum recapture durations when study 1 and 2 data were combined. The maximum longevity of any individual, therefore, would be an individual captured on the first day of study 1, May 30th 1995, and last captured on August 26th 1995, a period of 89 days. These records of the potential longevity of individuals are obviously strongly influenced by the temporal and spatial restrictions of the studies.

6.2.2. Effects of marking and handling

An analysis of the effects of marking and handling on individuals captured and recaptured in these studies was carried out using two well-established (methods 1 and 2 below) and one original method (method 3 below).

1) The first method was simply to look at the number of individuals recaptured. Low recapture frequencies are thought to indicate strong marking and handling effects (Morton 1982, Morton 1984). This is highly subjective and difficult to test statistically, but nevertheless informative to compare interspecific differences.

2) If the probability of an insect being caught on any sampling occasion remains constant, then the number of successive recaptures, regardless of previous captures, should conform to the Poisson distribution for a particular sample size and mean. A significant deviation from the expected values may indicate a tendency for marked individuals to be recaptured more or less often than expected. Expected values for frequencies of recaptures were calculated (Sokal and Rohlf 1981) and compared with the observed values (Table 6.4) for species which had five or more recaptures.

3) When an individual was captured in a fruit trap, it was either a new capture or a recapture. If a new capture it would then have been uniquely marked, had a forewing length measurement taken from base to apex, an assessment of wing damage and

condition made, and then released. If a recapture it would then have been identified from its unique mark, an assessment of wing damage and condition made, and then released. New captures were handled longer than recaptures. An assumption was made that the distance flown upon release was proportional to the handling time. It was also assumed that the handling process for each individual captured was identical (controlled to some degree by using one investigator, although this is slightly flawed as through experience the investigator should become more skilled and quicker at this handling process), so that any difference in stress induced through handling was due to length of handling time rather than the specific peculiarities of each handling experience. Estimations of the distance flown by individuals when released from fruit traps was noted at the time of capture for many individuals (but not all, due to the time consuming nature of this procedure). The mean distance flown by individuals of each species when released after first capture was then compared with the mean distance flown after recaptures.

The relationship of mean forewing length and mean distance flown upon release was investigated for all species encountered. The mean and range of wing measurements of Trinidadian species, were then compared with those for the same species, if found, in Costa Rica (DeVries 1987, DeVries 1988).

6.3. Results

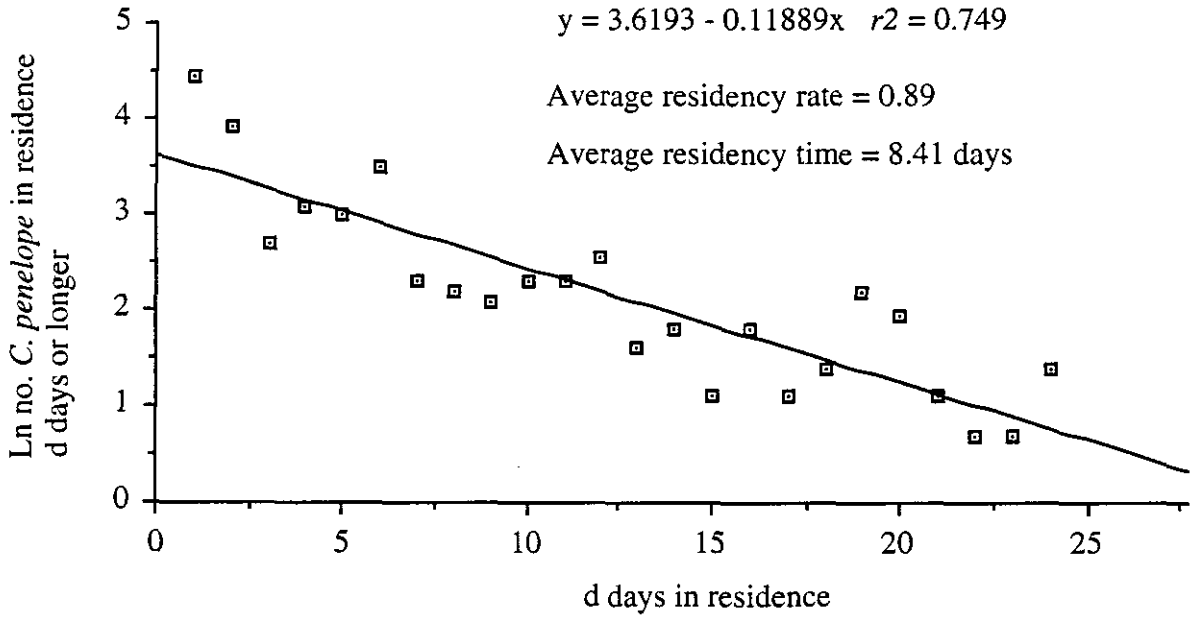
6.3.1. Residency rates and times

The example recapture duration decay plot (Fig. 6.1), used to calculate the residency rate of *C. penelope* in study 2, shows the gradient of the regression line ln ϕ to be -0.119, the residency rate ϕ, therefore being 0.89. This gives an average residency time of 8.41 days.

This was the longest average residency time calculated for *C. penelope*, compared with 4.42 days for study 1 (Table 6.1) and 7.93 days when the study 1 and study 2 data were combined. The two site replicates in study 1 showed different average residency times of 3.65 days for site 1 and 1.71 days for site 2 (Table 6.1).

For *Morpho peleides*, the longest average residency time was produced by the males in study 1, 11.97 days, compared with 4 days for the females in the same study (Table 6.1). This difference in average residency time between the sexes was not so evident from study 2 (3.1 days for males versus 2.4 days for the females). Average residency time when the data for the two sexes was combined, was greater in study 1 (6.64 days) than study 2 (3.63 days) (Table 6.1).

Figure 6.1. Recapture duration decay plot for *C. penelope* (males and females combined) in study 2



6.3.2. Estimates of population sizes

Calculated half and whole-day population estimates followed similar population fluctuation patterns, hence only one example is given, that for *C. penelope* in study 1, site 1 (Fig. 6.2a). The pattern of whole-day population estimate fluctuations over the course of this study (and all other studies investigated) were also found to follow closely the mean population estimates derived from the two half-day estimates. Hence only one example is shown here, again for *C. penelope* in study 1, site 1 (Fig. 6.2b), and in subsequent cases, only graphs of half-day population estimates with confidence limits are shown.

The populations of *C. penelope* in site 1 (Fig. 6.3a) and site 2 (Fig. 6.3b) (separated by 500 m) of study 1, appeared to show different patterns of population fluctuations over the same 23.5 day period. In study 1, site 1, the five highest *C. penelope* population peaks occurred on day 8.5 (c.70 individuals), 11.5 (c.50), 13.5 (c.80), 14.0 (c. 90 individuals) and 20 (c. 55). In study 1, site 2, peaks were found on days 14.5 (c.80

individuals), 16.0 (c. 50), 18.5 (c. 80), 19.5 (c. 130) and 21.0 (c. 50). Hence *C. penelope* in site 1 had four of its five highest population estimate peaks before site 2 had its first (Fig. 6.3a&b). No significant correlation was found between the half-day population estimates at the two sites ($r=-0.008$, $df=43$, $p>0.05$), although a significant positive correlation was found between the total of new and recaptured *C. penelope* individuals in site 1 and site 2 ($r=0.635$, $df=24$, $p<0.01$).

Higher half-day population estimates of *C. penelope* were found in study 2 (Fig. 6.5) than in study 1 (Fig. 6.4). In study 1, 11 out of the 47 half-day population size estimates were greater than 100, 2 of which were greater than 200. In study 2, 33 out of the 45 half-day population size estimates were greater than 100, 14 of which were greater than 200. The total sum of the half-day population size estimates for study 1 (sites 1 and 2) was 2779 and for study 2 was 8046 (Table 6.1). The total number of individuals this represented was estimated at being 563 for study 1 and 902 for study 2 (Table 6.1).

Population size estimates for *Morpho peleides* also revealed greater half-day population estimates in study 2 (Fig. 6.6.b) than study 1 (Fig. 6.6.a), with total population size estimates of 163 and 53 over the course of each of these respective studies (Table 6.1).

Half-day population size estimates of *Colobura dirce* were between 0 and 16 individuals in study 1 (Fig. 6.7.a) and between 0 and 48 in study 2 (Fig. 6.7.b). For *Taygetis andromeda* these estimates ranged between 0 and 81 (Fig. 6.7.c), and for *Cissia hermes* between 0 and 96 in study 2 (Fig. 6.7.d). Insufficient data were available for estimation of the relevant residency rates and therefore population size over the duration of the study (only three points were available for the recapture duration decay plots).

Table 6.1. Estimates of residency rate (ϕ), residency time (days) and overall population size over relevant study periods, 23.5 days for study 1 and 22.5 days for study 2, using the Jolly-Seber method. Estimates come from study 1 (comprising sites 1 and 2) and study 2.

Species	Study (sites)	Residency rate ϕ	Regression coefficient r^2	Day specific loss rate $1-\phi$	Mean expected residence (Days)	Total estimated population ΣN_i (Jolly-Seber)	Estimated total brood number Jolly-Seber
Cissia penelope	1 (1)	0.760	0.607	0.240	3.65	947	227
Cissia penelope	1 (2)	0.558	0.950	0.442	1.71	873	386
Cissia penelope	1 (1&2)	0.798	0.761	0.202	4.42	2779	563
Cissia penelope	2	0.888	0.749	0.112	8.41	8046	902
Cissia penelope	1 &2	0.882	0.807	0.118	7.93	-	-
Morpho peleides (f)	1 (1&2)	0.781	0.546	0.219	4.04	-	-
Morpho peleides (m)	1 (1&2)	0.920	0.203	0.080	11.97	-	-
Morpho peleides (m&f)	1 (1&2)	0.860	0.137	0.140	6.64	379	53
Morpho peleides (f)	2	0.660	0.900	0.340	2.40	-	-
Morpho peleides (m)	2	0.723	0.568	0.277	3.08	-	-
Morpho peleides (m&f)	2	0.759	0.730	0.241	3.63	677	163
Morpho peleides (m&f)	1&2	0.873	0.486	0.127	7.37	-	-

Figure 6.2.a. Comparison of Jolly-Seber population estimates of *C.penelope* in Study 1, site 1, for half-day data and whole-day data

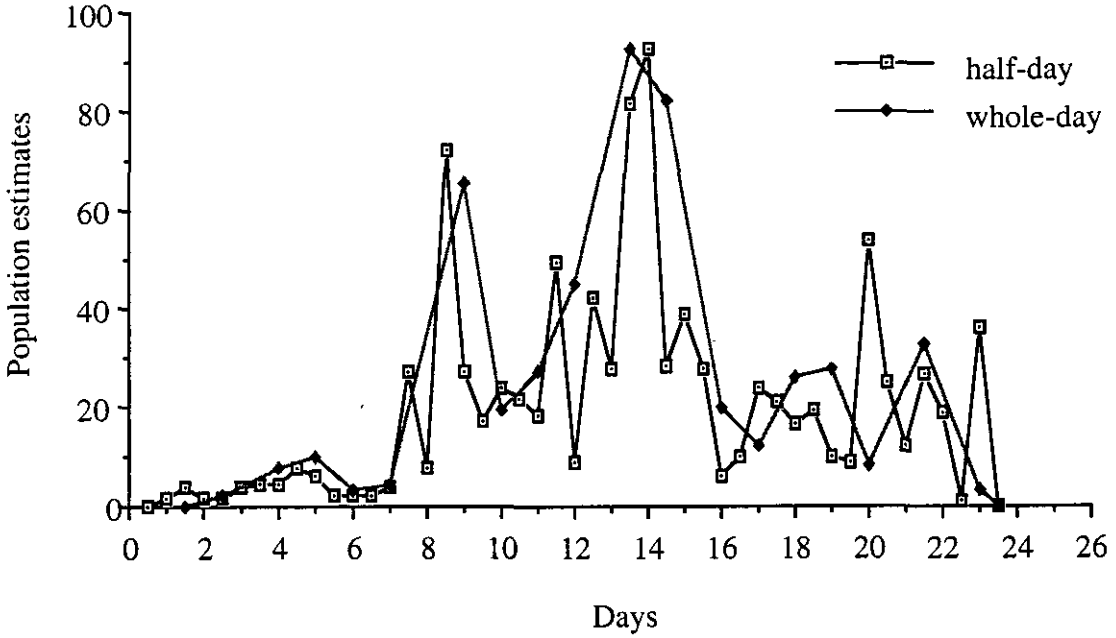


Figure 6.2.b. Comparison of Jolly-Seber population estimates for *C.penelope* using whole-day data and means of two half-days

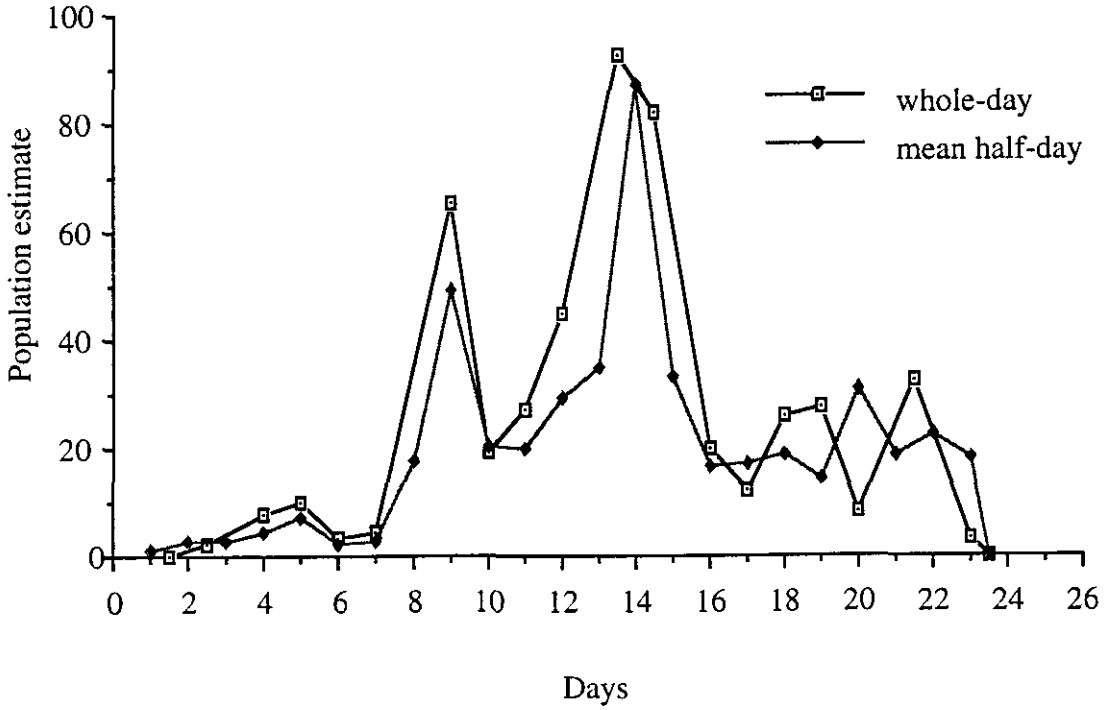


Figure 6.3a. Half-day population estimates of *C. penelope* in site 1, study 1, with 95 % confidence limits.

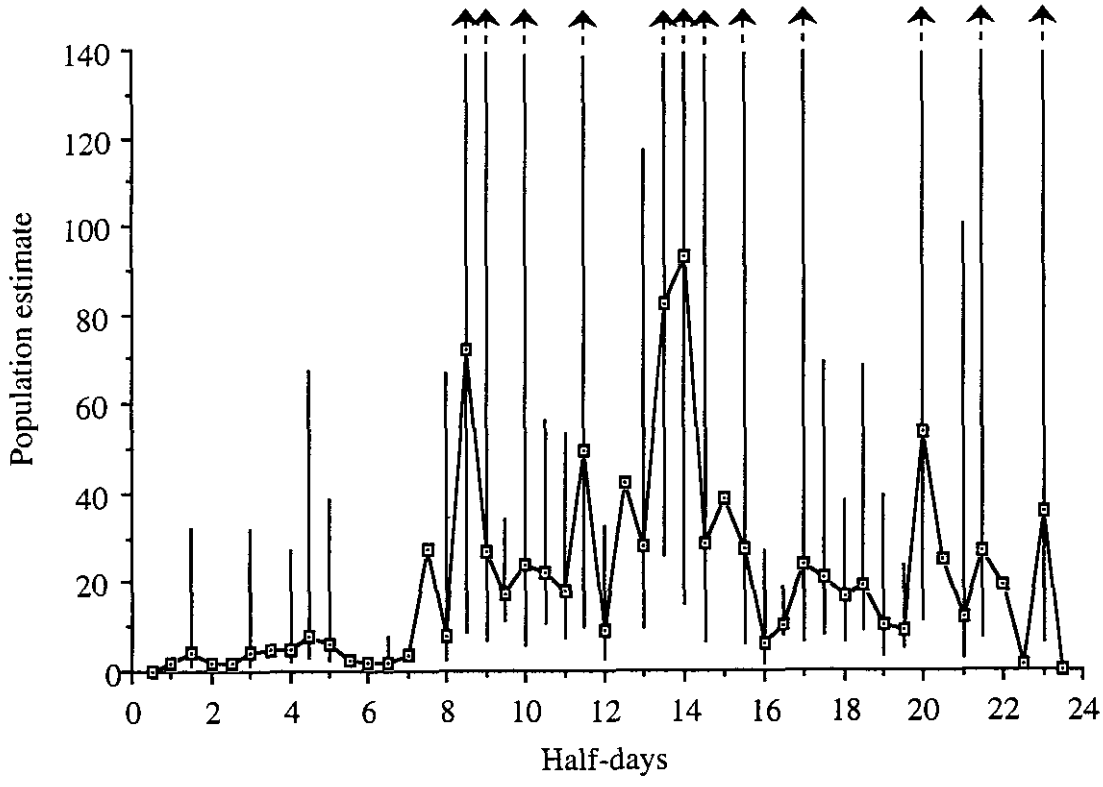


Figure 6.3b. Half-day population estimates of *C. penelope* in site 2, study 1, with 95 % confidence limits.

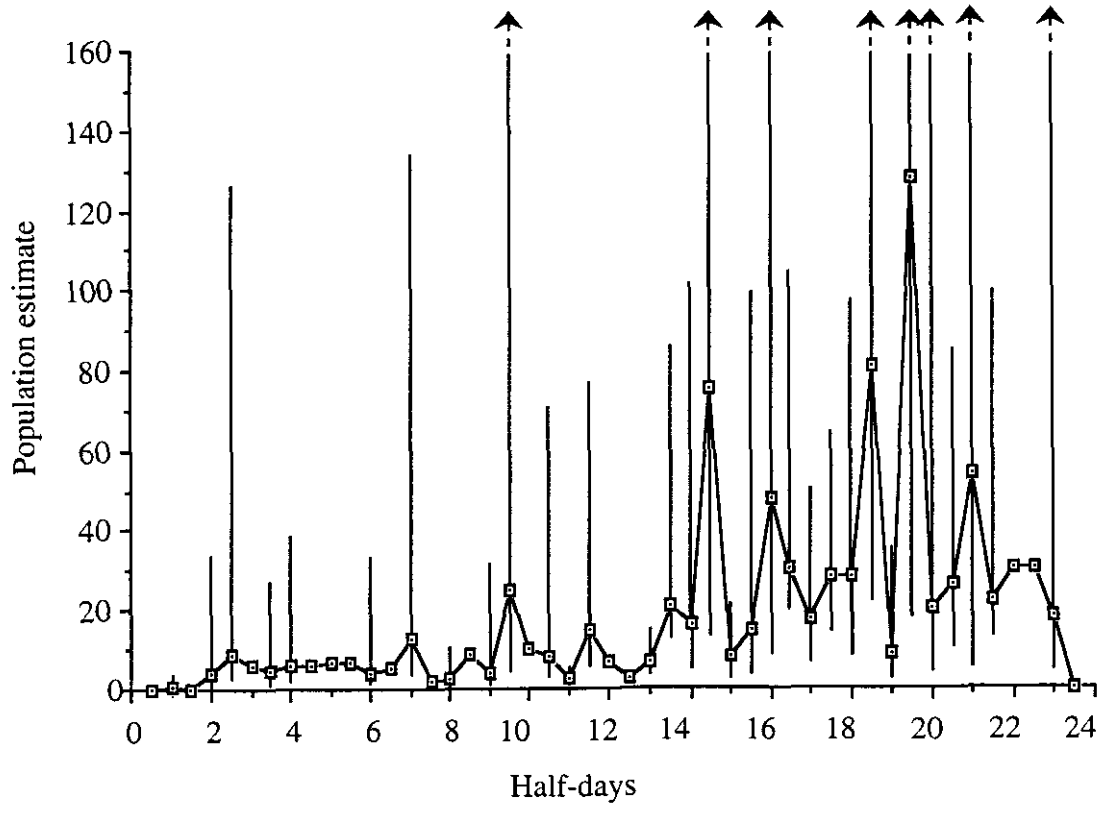


Figure 6.4. Half-day population estimates of *C. penelope* in study 1 (sites 1 and 2 combined), with 95 % confidence limits.

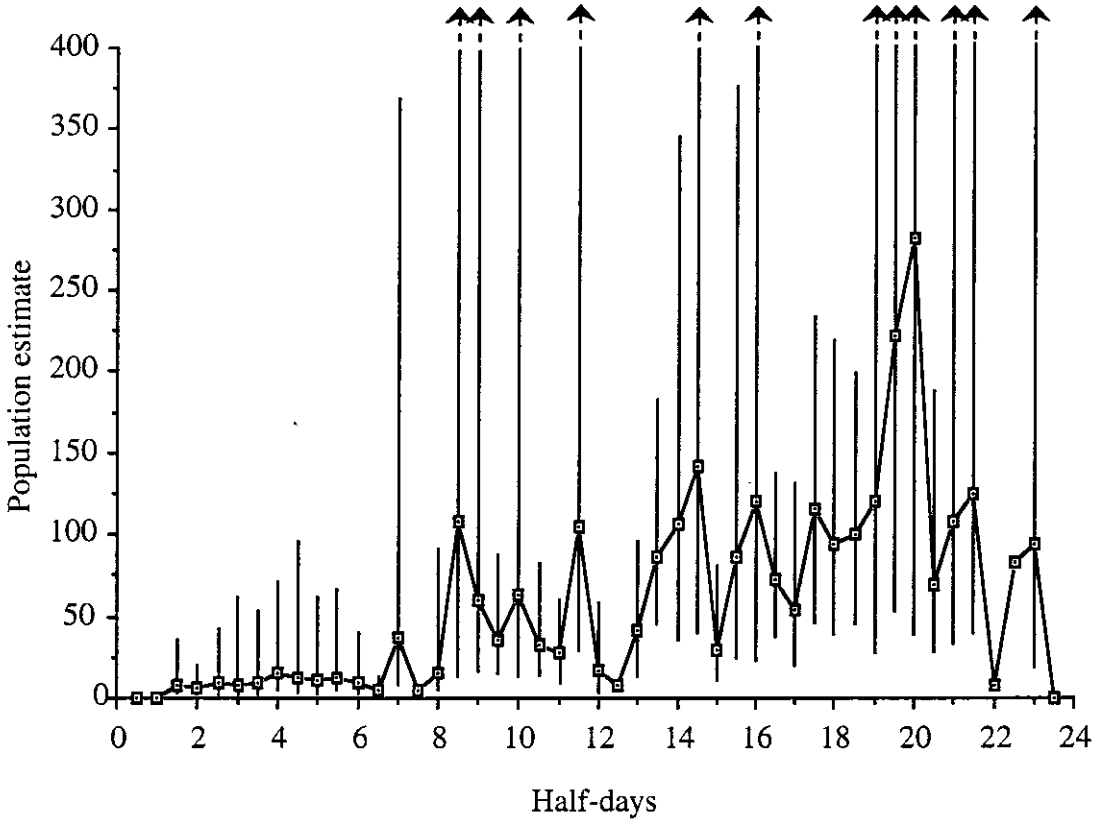


Figure 6.5. Half-day population estimates for *C. penelope* in Study 2, with 95 % confidence limits.

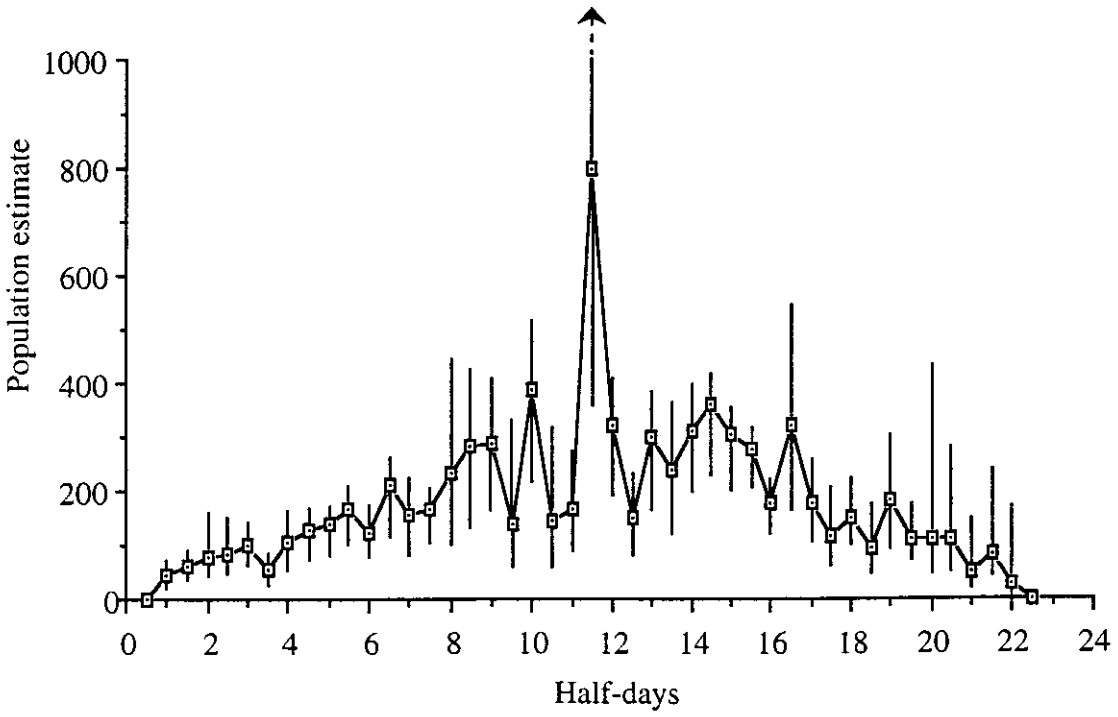


Figure 6.6.a. Half-day population estimates for *Morpho peleides* in study 1 (sites 1&2), with 95 % confidence limits

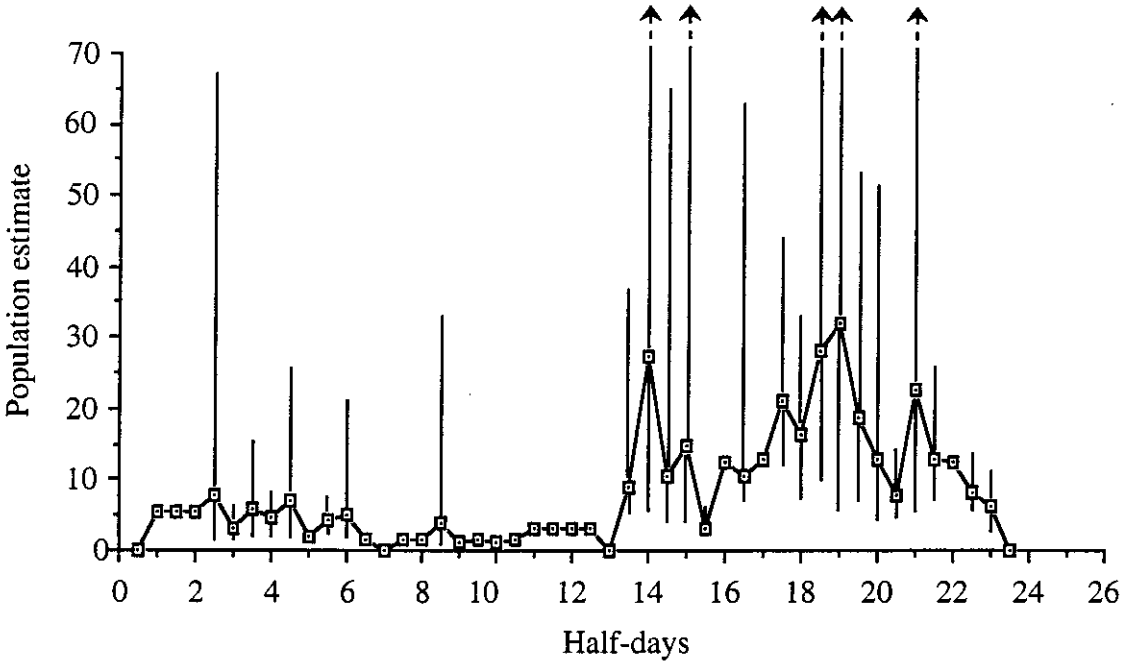
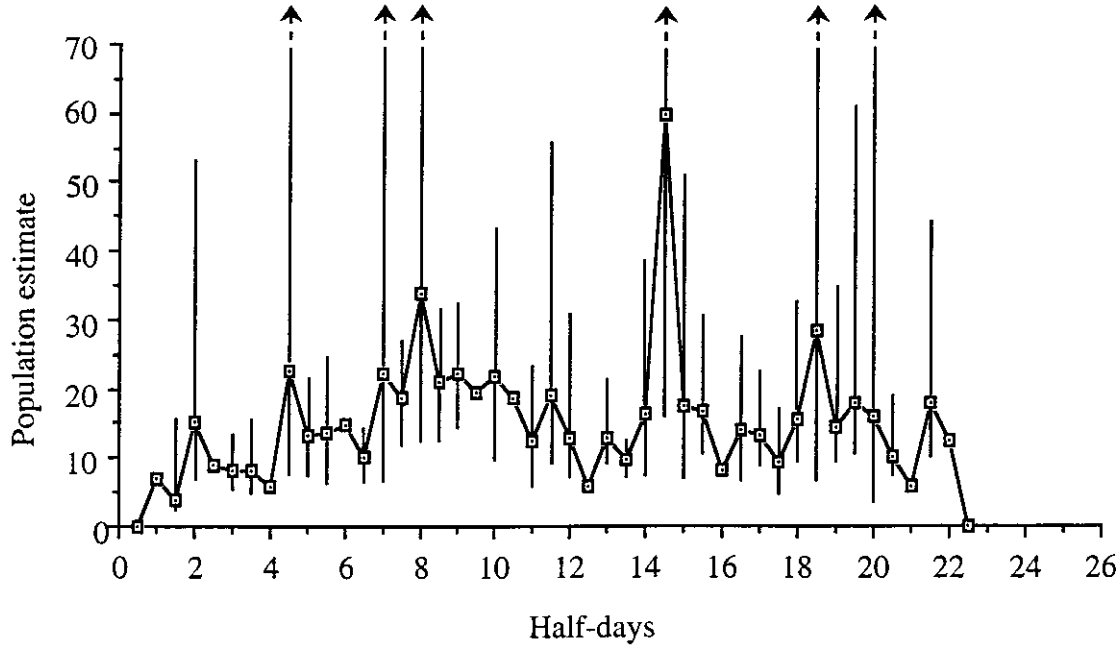


Figure 6.6.b. Half-day population estimates for *Morpho peleides* in study 2, with 95 % confidence limits



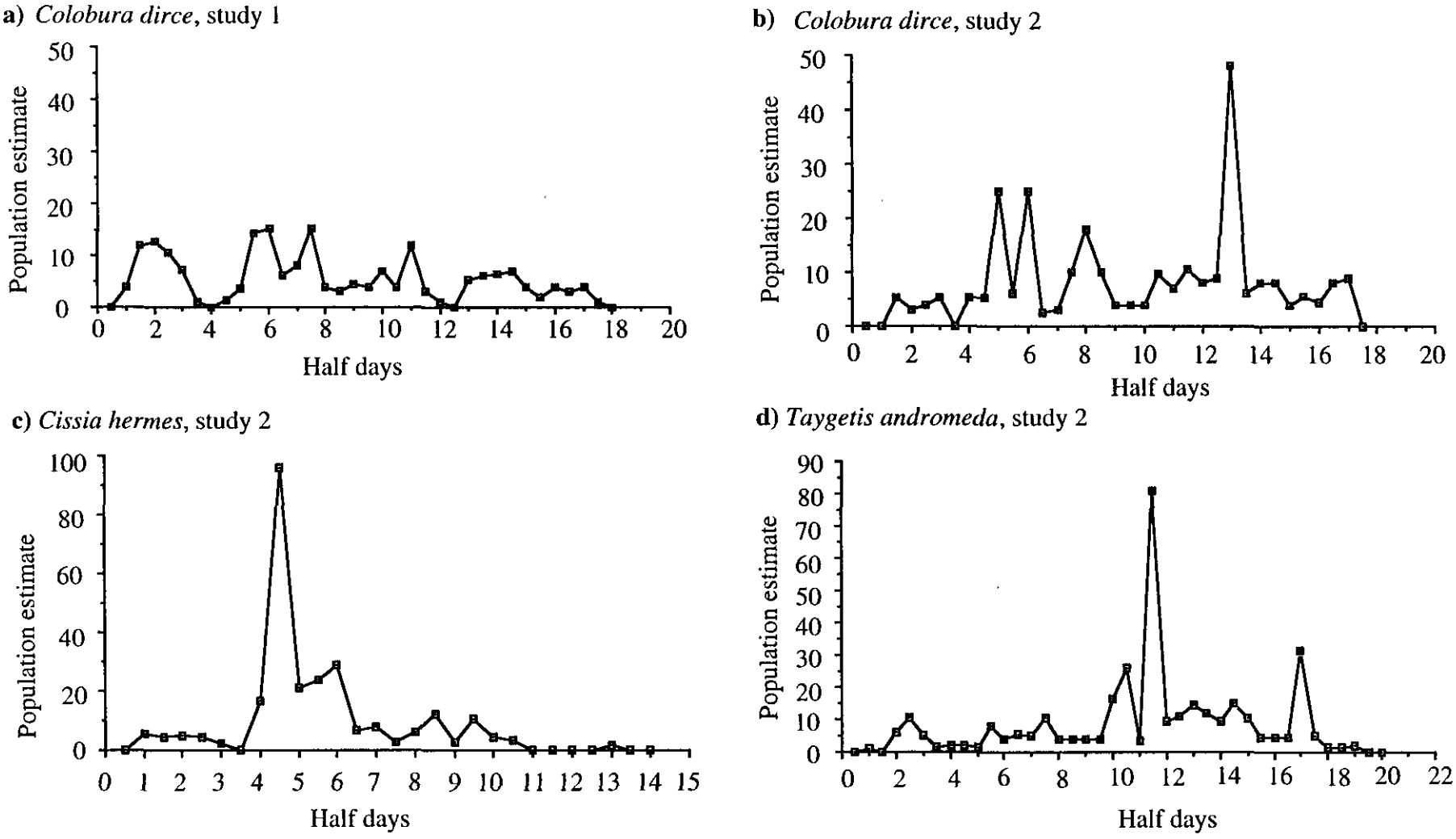


Figure 6.7. Half-day population estimates for **a)** *Colobura dirce* in study 1, **b)** *Colobura dirce* in study 2, **c)** *Cissia hermes* in study 2 and **d)** *Taygetis andromeda* in study 2.

The greatest record of longevity shown by any fruit-feeding species in this study was 66 days (9.5 weeks) by *Cissia penelope* (Table 6.2). The next longest lived (resident) *C. penelope* individual was present in the study area for 34 days. Several species also remained resident in the study area for about 30 days, including *Morpho peleides* (male), *Taygetis andromeda*, *Colobura dirce*, *Caligo eurilochus* and *Memphis eribotes*. Several others were present for about 15 days including *Cissia hermes*, *C. hesione*, *C. myncea*, *Archaeoprepona demophon* and *Taygetis virgilia*. The last group of residents stayed less than 6 days, such as *Cissia arnaea*, *C.renata*, *Pierella hyalinus*, *Catoblepia berecynthia* and *Hamadryas feronia*.

Table 6.2. Maximum longevity of individuals captured in study 1 and 2 combined.

Species	Longevity (Days)	Date and time
Cissia penelope (i)	66.0	31/5/95 pm to 5/8/95 pm
Caligo eurilochus (f)	34.5	4/7/95 am to 7/8/95 pm
Cissia penelope (ii)	34.0	26/6/95 pm to 30/7/95 am
Morpho peleides (m)	31.0	4/7/95 pm to 4/8/95 pm
Taygetis andromeda	30.0	7/7/95 pm to 6/8/95 pm
Colobura dirce	29.0	11/7/95 pm to 9/8/95 pm
Memphis eribotes	28.0	30/5/95 pm to 27/6/95 pm
Cissia hesione	16.0	13/7/95 am to 29/7/95 am
Taygetis virgilia	15.5	15/7/95 am to 30/7/95 pm
Cissia myncea	15.0	15/7/95 pm to 30/7/95 pm
Archaeoprepona demophon	13.5	1/6/95 pm to 15/6/95 am
Cissia hermes	13.0	9/7/95 pm to 22/7/95 pm
Cissia arnaea	5.5	24/7/95 pm to 30/7/95 am
Cissia renata	5.5	28/6/95 pm to 4/7/95 am
Catoblepia berecynthia	5.0	5/8/95 am to 10/8/95 am
Pierella hyalinus	4.0	19/6/95 pm to 23/6/95 pm
Hamadryas feronia	2.0	5/7/95 pm to 7/7/95 pm

6.3.3. The effects of marking and handling

a) Percentage of individuals recaptured

In study 1, the percentage of individuals which were recaptured varied from 15.4 % for *C. hermes* to 47.1 % for *Colobura dirce* (Table 6.3). In study 2, the values ranged from 12.1 % for *C. hermes*, to 61.7 % for *Morpho peleides*. Of the five species in both study 1 and 2, *C. hermes* and *Colobura dirce* had a higher percentage of marked individuals recaptured in study 1 than study 2 (15.4 % and 12.1% for *C. hermes* and

47.1 % and 26.8 % for *Colobura dirce*, in each of these studies respectively). The other three species all had higher numbers of individuals recaptured in study 2 than study 1 (39.8 % and 28.6 % for *C. penelope*, 60.8 % and 43.9 % for the *Caligo* species and 61.7 % and 43.9 % for *Morpho peleides*, Table 6.3). When the proportion of individuals recaptured in study 1 was compared with that found in study 2, for the 14 species (or species groups for *Caligo*) in Table 6.3, only *C. penelope* showed a significant difference (G=4.83, df=1, $p<0.05$).

Table 6.3. Number of individuals marked and percentage recaptured, for each species with more than 10 individuals marked in either study 1 or study 2. G-test values shown for comparison between % recaptured in each study (NS = Not significant, * = $p<0.05$).

Species	Study 1		Study 2		G-test
	Inds. marked	Percent recs.	Inds. marked	Percent recs.	
Morpho peleides	57	43.9	81	61.7	1.32 NS
Caligo species	68	43.9	97	60.8	1.39 NS
Catoblepia berecynthia	10	30.0	14	50.0	0.42 NS
Cissia penelope	231	28.6	893	39.8	4.84 *
Opsiphanes cassina	22	36.4	2	50.0	0.06 NS
Cissia hesione	14	14.3	42	42.9	2.24 NS
Colobura dirce	51	47.1	71	26.8	2.51 NS
Cissia myncea	8	37.5	37	32.4	0.04 NS
Taygetis andromeda	11	27.3	75	32.0	0.06 NS
Taygetis virgilia	7	14.3	23	30.4	0.49 NS
Pierella hyalinus	11	18.2	4	25.0	0.05 NS
Hamadryas feronia	0	0	19	15.8	-
Cissia hermes	39	15.4	102	12.1	0.25 NS
Archaeoprepona demophon	15	6.7	3	0	-

When an overall percentage of individuals recaptured for the two studies was calculated, it was found that for the 14 species with at least 10 individuals marked in either study, two species (*Morpho peleides* and the *Caligo* species) had more than 50 % of marked individuals recaptured, one species (*Catoblepia berecynthia*) > 40 %, six species (*C. penelope*, *O. cassina*, *C. hesione*, *Colobura dirce*, *C. myncea*, *T.*

andromeda) > 30 %, two species (*T. virgilia, Pierella hyalinus*) > 20 %, two species (*Hamadryas feronia, C. hermes*) > 10 % and one species (*A. demophon*) < 10 % of its marked individuals recaptured (Table 6.3).

b) Observed recapture frequencies versus expected

The results varied from species to species and were not always consistent between studies 1 (Table 6.4.a) and 2 (Table 6.4.b). Of the six species examined in study 1, three species showed no significant difference between observed and expected recapture frequencies (*Cissia hermes*, *Colobura dirce* and *Morpho peleides*) whilst three species (or group of species in the case of the three *Caligo* species) were significantly different (Table 6.4.a). The *Caligo* genus had more individuals not recaptured than expected and less recaptured in other recapture frequency classes ($G=38.4$, $df=2$, $p<0.001$), *Cissia penelope* had more individuals not recaptured and recaptured twice or more than expected and less recaptured once than expected ($G=10.36$, $df=2$, $p<0.01$), whilst *Opsiphanes cassina* had more individuals not recaptured than expected and less than expected recaptured once or more ($G=7.91$, $df=1$, $p<0.01$). In both study 1 and 2, five species were examined. *Cissia penelope* was significantly different from the expected Poisson distribution of recapture frequencies in study 1 (see above) and study 2 ($G=184$, $df=2$, $p<0.001$). A significant difference was also found for the *Caligo* species in both studies ($G=38.4$ and 17.4, $df=2$, $p<0.001$). *Cissia hermes* ($G=0.04$, $df=1$, $p>0.05$), *Colobura dirce* ($G=3.64$, $df=2$, $p>0.05$) and *Morpho peleides* ($G=3.67$, $df=2$, $p>0.05$), however, were not significantly different from expected Poisson distribution values in study 1 but were all significantly different in study 2 ($G=10.5$, $df=1$, $p<0.01$; $G=9.64$, $df=2$, $p<0.01$; $G=10.26$, $df=2$, $p<0.01$, for each species respectively) (Table 6.4.b).

Of the species examined only in study 2, *Cissia hesione*($G=2.78$, $df=2$, $p>0.05$), *Catoblepia berecynthia* ($G=0.52$, $df=1$, $p>0.05$), *Taygetis virgilia* ($G=0.21$, $df=1$, $p>0.05$) and *Hamadryas feronia* ($G=0.63$, $df=1$, $p>0.05$) showed no significant

difference between observed and expected recapture frequencies. Species which did show significant differences were *Cissia myncea* (G=6.08, df=2, p<0.05) and *Taygetis andromeda* (G=12.98, df=2, p<0.01) (Table 6.4.b).

Table 6.4.a. Observed recapture frequencies and expected recaptures from Poisson distribution in study 1.

	Recapture frequency	Observed	Expected	G-test
Cissia penelope	0	165	151.8	G=10.36 **
	1	44	63.7	
	2+	22	15.5	
Cissia hermes	0	33	33.4	G=0.04
	1+	6	5.6	
Caligo species	0	37	14.3	G=38.4 ***
	1	9	21.9	
	2+	20	29.9	
Colobura dirce	0	27	21.1	G=3.64
	1	13	18.6	
	2+	11	11.2	
Opsiphanes cassina	0	14	11.1	G=7.91 *
	1+	8	10.9	
Morpho peleides	0	32	25.0	G=3.67
	1	15	20.6	
	2+	10	11.4	

Table 6.4.b. Observed recapture frequencies and expected recaptures from Poisson distribution in study 2.

	Recapture frequency	Observed	Expected	G-test
Cissia penelope	0	538	357.3	G=184 ***
	1	161	327.3	
	2+	194	208.4	
C. hermes	0	91	78.3	G=10.5 **
	1+	11	23.7	
C. hesione	0	24	19.6	G= 2.78
	1	10	14.9	
	2+	8	7.5	
C. myncea	0	25	19.3	G= 6.08 *
	1	6	12.5	
	2+	6	5.1	
Caligo species	0	38	20.0	G= 17.4 ***
	1	25	31.6	
	2+	34	45.4	
Morpho peleides	0	31	18.6	G= 10.26 **
	1	25	27.4	
	2+	25	35.0	
Catoblepia berecynthia	0	7	5.9	G= 0.52
	1+	7	8.0	
Taygetis andromeda	0	51	37.0	G= 12.98 **
	1	13	26.1	
	2+	11	11.9	
T. virgilia	0	16	17.0	G= 0.21
	1+	7	6.0	
Colobura dirce	0	52	44.6	G= 9.64 **
	1	10	20.7	
	2+	9	5.7	
Hamadryas feronia	0	16	14.6	G= 0.63
	1+	3	4.4	

c) Distance flown by new captures compared with recaptures

The mean distance flown by individuals when released after being captured for the first time was compared with the mean distance flown upon release for recaptured individuals of the same species (Table 6.5). The results showed that of the nine species with a sufficient sample size (≥3), seven species showed no significant differences. *Opsiphanes cassina* was found to fly significantly further from first captures than recaptures ($t=2.32$, $df=15$, $p<0.05$) and *Catoblepia berecynthia* flew significantly further from recaptures than first captures ($t=2.69$, $df=10$, $p<0.05$) (Table 6.5).

Table 6.5. Mean distances flown upon release for new captures and recaptures. Individuals which were not sexed were included in the total *Morpho peleides* (m&f) sample, hence sample sizes are larger than the sum of female and male sample sizes. T-test values are shown in the last column

Species	New (n) or recapture (r)	N	Mean distance flown (m)	S.d.	Significance (n versus r)
Pierella hyalinus	n	9	5.5	5.61	t=0.28 NS
	r	3	4.5	4.77	
T. andromeda	n	22	2.16	1.35	t=0.01 NS
	r	6	2.17	1.60	
Cissia hermes	n	59	2.03	1.58	t=0.06 NS
	r	8	2.00	1.10	
C. penelope	n	343	2.06	1.92	t=1.17 NS
	r	127	2.30	2.01	
Eryphanis automedon	n	5	4.0	1.73	t=0.80 NS
	r	8	3.44	0.82	
Catoblepia berecynthia	n	11	5.36	3.56	t=2.69 *
	r	3	12.67	6.43	
Opsiphanes cassina	n	16	13.63	9.74	t=2.32 *
	r	11	5.96	5.93	
Morpho peleides (m)	n	33	11.49	13.60	t=0.83 NS
	r	17	8.53	7.76	
Morpho peleides (f)	n	17	15.71	12.27	t=1.27 NS
	r	10	9.65	11.47	
Morpho peleides (both m&f)	n	53	12.98	12.97	t=1.67 NS
	r	36	8.74	9.78	
Colobura dirce	n	42	6.68	5.71	t=1.997 NS
	r	32	4.59	1.75	

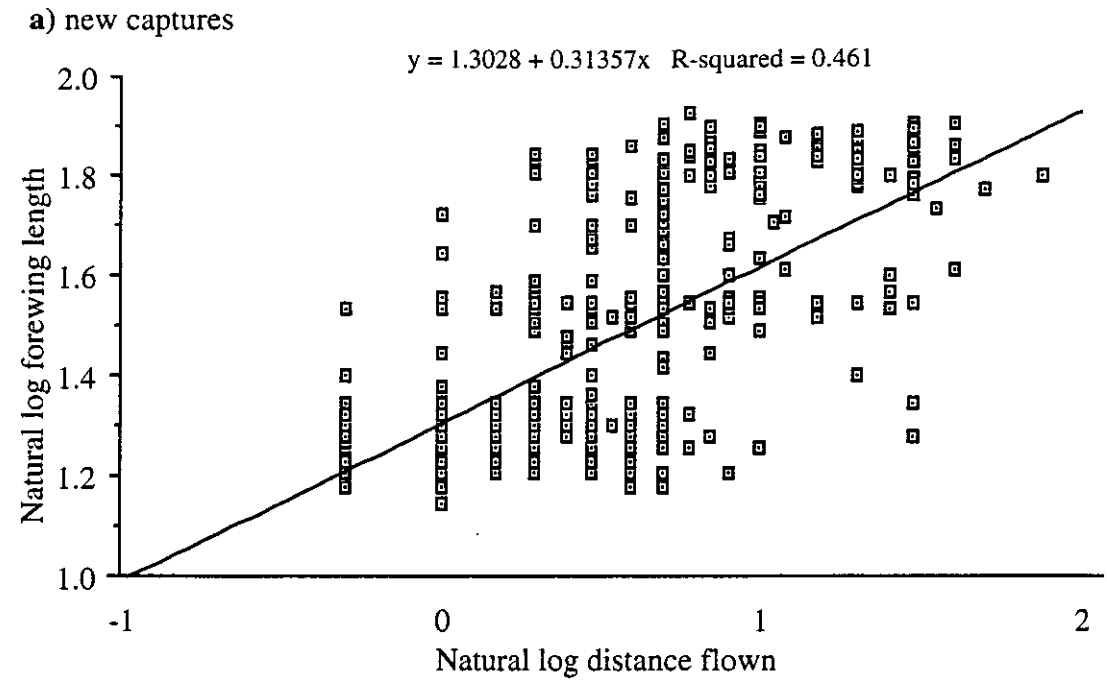
d) Forewing length compared with distance flown

The mean and range of forewing lengths of species encountered in the course of fieldwork in Trinidad were recorded (Table 6.6). Mean and range of forewing lengths were also available for the same species or subspecies taken from Costa Rica (DeVries 1987, DeVries 1988).

A highly significant positive relationship between forewing length and distance flown after release was found for new captures (Fig. 6.8.a; $r^2=0.461$, $F=560.14$, $p<0.0001$) and recaptures (Fig. 6.8.b; $r^2=0.412$, $F=165.4$, $p<0.0001$), for all individuals where information on forewing length and distance flown had been recorded.

Table 6.6. Forewing length measurements of species captured in fruit traps in 1995 in Trinity Hills, South-East Trinidad, compared with measurements from Costa Rica. Winglength ranges in parentheses from DeVries (1987) and mean winglength values, and associated number in the sample, in parentheses, from DeVries (1988).

Species	N	Winglength Range (mm)	Winglength Mean (mm)	S.E.
A. amphimachus	2	58-60	59	1.41
A. demophon (CR)	16 (9)	52-68 (54-60 ssp)	58.44 (55.5)	4.69
A. demophoon	1	(54-58 ssp)	58	
P. omphale (CR)	1 (7)	(50-55 ssp)	61 (48.4)	
C. arnaea	8	18-21 (19-23)	19.44	0.98
C. brixiola	1		16	
E. cephus (m)	2	20-22	21	1.41
C. junia	1		24	
C. libye	2	25-27 (22-24)	26	1.41
C. hesione (CR)	27 (7)	17-21 (18-21)	19.52 (20.8)	1.16
C. myncea	20	16-22	19.3	1.84
C. hermes	97	14-20 (16-20)	17.23	1.31
C. penelope	529	18-23	20.44	0.95
Pierella hyalinus	12	33-39	35.42	1.51
T. andromeda (CR)	39 (8)	31-37 (33-37)	34.08 (34.1)	1.24
T. virgilia	11	31-39 (37-41ssp)	36.27	2.37
T. penelea	5	28-34 (26-29)	30.4	2.19
T. echo	1		36	
Catoblepia berecynthia	17	44-53	48.82	2.33
Eryphanis automedon	5	51-64	56.8	5.12
O. cassiae	10	35-46	42	3.50
O. cassina (CR)	20 (11)	34-43 (36-40 ssp)	36.65 (36.65)	2.91
Morpho peleides (m)	51	58-70	63.1	2.9
Morpho peleides (f)	24	64-77	70.625	3.27
Morpho peleides (CR)	75 (12)	58-77 (64-78 ssp)	65.51 (71.3)	4.64
C. eurilochus (CR)	(9)	(77-91 ssp)	(81.6)	
Colobura dirce	81 (7)	22-37 (35-37)	31.96 (32.5)	4.20
Pyrrhogyra tipha	1		26	
Temenis laothoe	2	28-29 (27-29 ssp)	28.5	
Catagramma astarte	1		25	
Historis acheronta	1		43	
Hamadryas feronia	4	35-40 (35-38 ssp)	37	2.45
Zaretis itys (CR)	1 (7)	(33-36)	31 (35.1)	
Memphis eribotes	4	25-28	26.25	1.26
Memphis morvus (CR)	1 (8)	(29-32 ssp)	32 (32.4)	
Ithomia pellucida	1		24	



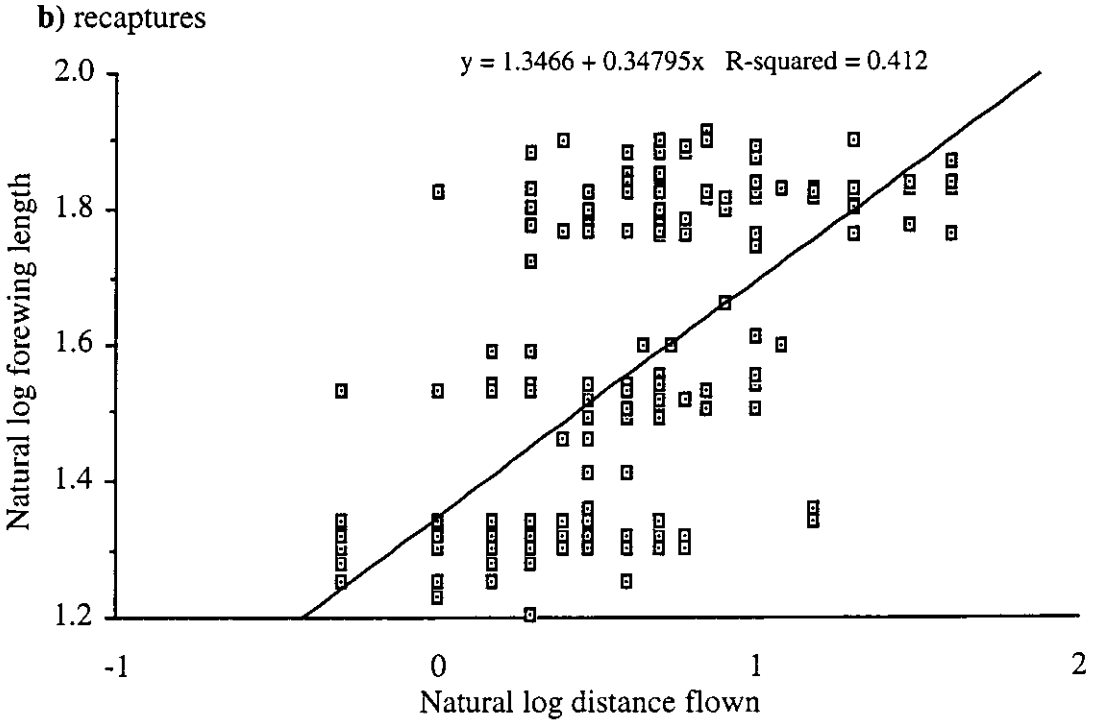


Figure 6.8. Natural log of forewing length against natural log distance flown of **a)** new captures and **b)** recaptures

6.4. Discussion

Cissia penelope was found to have average residency times of 1.71 and 4.42 days in study 1 and 8.41 days in study 2. The average residency times of *Morpho peleides* (male and female data combined) was 6.64 days in study 1 and 3.63 days in study 2. Male *Morpho peleides* were found to have higher average residencies than females (11.97 days compared with 4.04 days in study 1 and 3.08 days compared with 2.4 days in study 2), although in both cases r^2 values were much lower in the male *Morpho peleides* recapture duration decay regressions.

The average residency times in the present study are of a similar order of magnitude to those found for temperate butterfly species (Table 6.7). Average residency times were not found in the literature for tropical butterfly species.

Table 6.7. Examples of average residency times for temperate butterfly species from published sources.

Species	Habitat	Residency (days)	Study
Ringlet *Aphantopus hyperantus*	Woodland glades, U.K.	3.97 - 4.6	(Sutcliffe *et al.* 1997)
Heath fritillary *Mellicta athalia*	Woodland glades, U.K.	2.72 - 10.8	(Warren 1987b)
Sulfur butterfly *Colias alexandra*	Montane grassland, U.S.A.	1.9 - 11.5	(Watt *et al.* 1977)
Sulfur butterfly *Colias meadii*	Subalpine/alpine grassland, U.S.A.	3.7 - 6.6	(Watt *et al.* 1977)
Black swallowtail *Papilio polyxenes*	Hay fields, U.S.A.	4.75 - 16.2	(Lederhouse 1983)

Cissia penelope and *Morpho peleides* were abundant enough to estimate average residency rates from recapture duration decay plots and, therefore, an estimate of population size over the duration of the study. The fact that other species were not recaptured in sufficient abundance to allow similar population structure analysis was probably due to (a) the small area covered by the grids of fruit traps which did not cover all movements of individuals, which therefore effectively emigrated, (b) the short

duration of the trapping period relative to species' average longevities, and (c) the fact that butterfly assemblages tend to consist of several dominant species and many less abundant ones (which is exacerbated by habitat disturbance, see Ch.3).

The estimates of longevity (longest records of residency) reported here (Table 6.2) are estimates which are also constrained spatially by the area of the grid of fruit traps (i.e. not large enough to encompass the entire life-time movements of individuals), and restricted temporally by the duration of the study. Fruit trap studies at larger spatial and temporal scales would provide more information on the relative longevities of forest fruit-feeding butterfly species. The estimates from the present study, however, are the first from the field where predation and competition pressures also exist. In an example where these pressures have been removed, and the spatial and temporal limitations of the fruit trapping were not factors, a *Cissia hesione* individual was reported to have lived for over 4 months in a green house in Texas, and only died when accidentally trodden on (DeVries 1987). The longest-lived *C. hesione* individual in this study was 16 days although a *C. penelope* individual was encountered over a 9.5 week period. The longest residency recorded for a *Morpho peleides* male in the present study was 31 days, which compares well with that reported in a confined Costa Rican forest of 33 days (Young and Thomason 1974).

The use of Jolly-Seber methods to derive open population estimates for several species, proved successful in determining patterns of population fluctuation in two studies carried out over the same temporal scale but different spatial configuration. Although confidence limits were large, general patterns of fluctuations were discernable and average daily population sizes calculable.

Smaller population size estimates found in study 1 (between 0 and 128) compared with study 2 (between 30 and 800) for *C. penelope* populations, may be due to the different spatial arrangements of the 18 fruit traps in each study, or to the difference in timing of the two studies relative to the onset of the wet season (study 1 was at the start of the

wet season compared with study 2 which was five weeks later). If butterflies are at lower abundance in the dry season and at greater abundance in the wet season (DeVries 1987), then an increase in *C. penelope* population size with progression of the wet season would be expected.

One would expect an overall population size estimate over the duration of a study to be greater than the number of new individuals encountered in the study, taking into account those individuals which remained undetected and escaped capture. This was the case for study 1 for *C. penelope* where 231 individuals were marked over the duration of the study and the overall population size estimated at 563. Therefore, if this estimate was accurate, 59 percent of the population remained undetected in study 1. In study 2, however, only 0.1 percent of the population remained undetected, with 893 individuals being marked and the overall population size estimated to be 902.

The significant positive correlation found between the total *C. penelope* captures and recaptures each day in site 1 and 2 of study 1, suggests that the number of individuals encountered at each site were in part determined by a common abiotic factor such as hours of sunshine, temperature or rainfall. The fact that no correlation was subsequently found between the population size estimates of *C. penelope* in site 1 and site 2 of study 1 (Fig. 6.3a & b) was attributed to the large confidence limits surrounding these estimates.

Morpho peleides was found at much lower population levels within the same study areas, compared with *C. penelope*, with half-day estimates of between 0 and 32 and a total population estimate over the duration of study 1 of 53 (57 marked). For study 2 half-day estimates of between 4 and 60 and a total population estimate over the duration of the study of 163 (81 individuals marked) (Table 6.1). In a confined population in a pocket of Costa Rican forest in the dry season and over a much larger area (300 ha compared with 24.8 ha for study 1 and 12 ha for study 2), daily *Morpho peleides* population estimates of between about 60 and 100 individuals were found, with a total

population size over the 11 day duration of the study estimated at 115 individuals (100 individuals being marked) (Young and Thomason 1974).

Morton (1984), reported that high recapture frequencies and good fits to the Poisson distribution, often used in butterfly population work, were unreliable indicators of the suitability of a MRR technique. The recapture frequencies for the 14 species in study 1 and 2 with at least 10 individuals marked in either study were relatively high, with two species with over 50 % of its individuals recaptured, one species with over 40 %, six species with over 30 %, two species with over 20 %, two species with over 10 % and one species with less than 10 % of its individuals recaptured. Data from comparable fruit trapping studies are available for two species, *C.hermes* (Emmel 1970) and *Morpho peleides* (Young and Thomason 1974). A five day MRR study on two *Cissia hermes* populations in Trinidad, using hand-held nets to capture all observed individuals, revealed that 11.9 % of 59 marked individuals and 14 % of 57 individuals were recaptured (Emmel 1970). This compares well with 12.1 % and 15.4 % of *C.hermes* individuals recaptured in study 2 and 1 respectively. Emmel (1970) believed that individuals were disappearing from the grassy patches into adjacent cacao plantation as the daytime temperature increased.

The low recapture frequency for this species could indicate a nomadic pattern of movement throughout the adult's lifetime rather than maintaining a home range. *C. hermes* feeds on a wide range of adult resources from fallen forest fruits, to roadside nectar sources such as *Lantana camara* (it is the only *Cissia* species to feed as an adult on nectar) and on the flower spikes of "Bull grass" (*Paspalum fasciculatum* Willd. and *P. virgatum* L.) (personal observation). It is also a generalist in terms of larval hostplants, using a suite of at least 13 species of grass and sedge (Singer and Ehrlich 1993). This generalist feeding and suite of hostplant species may preclude the necessity to maintain a specific lifelong home range in this species. In contrast, *Heliconius melpomene* is a specialist both in terms of adult resources and larval hostplant. In order to ensure feeding on preferential and scarce *Anguiria* and *Warwickzencia* vines for

nectar and pollen, *H. melpomene* follow learnt routes daily to these resources, thereby maintaining a home range (Ehrlich and Gilbert 1973). *Passiflora laurifolia* is this species' exclusive larval hostplant in Trinidad (Barcant 1970). Other *Heliconius* species also exhibit specific home-range behaviour (Cook *et al.* 1976, Ehrlich and Gilbert 1973, Turner 1971), remaining resident in an area for several months following learnt routes to resources and returning to the same communal roosting sites each night. Home-range behaviour has also been reported for *Morpho peleides* in forest in Costa Rica (Young and Thomason 1974).

In an 11 day period, 77 % of marked *Morpho peleides* individuals were resighted at least once in an isolated forest patch (c. 300 ha) in Costa Rica, by workers netting individuals at fruit piles and noting marked individuals when encountered (Young and Thomason 1974). Again, this compares well with 43.9 % and 61.7 % in the present study, especially when the intensity of searching is taken into account. In Young's study, workers were checking the fruit piles all day throughout the 11 day period and netting any marked individuals encountered along the way, compared with twice daily checking of only the fruit traps in my study. In a previous study carried out by Young and workers using similar techniques over an unconfined and much larger area of mountainous wet forest on the Caribbean slopes of the Central Cordillera in Costa Rica, only 20 % of 105 individuals were resighted, over a two month period (Young 1973). These and other examples of recapture frequencies from Neotropical studies are shown in Table 6.8.

Table 6.8. Percentage recaptures of butterflies from tropical studies.

Species	**Captures (% recaptured)**	**Country**	**Study**
Cissia hermes	59 (11.9 %)	Trinidad	(Emmel 1970)
Cissia hermes	57 (14.0 %)	Trinidad	(Emmel 1970)
Morpho peleides	100 (77.0 %)	Costa Rica	(Young 1973)
Heliconius erato (males)	315 (31.7 %)	Trinidad	(Turner 1971)
Heliconius erato (females)	267 (32.2 %)	Trinidad	(Turner 1971)
Heliconius ethilla	960 (46.8 %)	Trinidad	(Ehrlich and Gilbert 1973)

Significant differences between observed recapture frequencies and those expected from the Poisson distribution were found in 10 out of the 17 Poisson distributions examined. In all of these 10 cases, more individuals were marked and not recaptured than expected (0 class) and less recaptured once than expected (1 class). This is probably due to the spatial and temporal restrictions of this study (see third paragraph in this discussion), with many marked individuals not remaining in the study area. The use of the Poisson distribution to test for randomness and independence between the numbers of recaptures in each recapture group, would be more effective in a more closed system where more marked individuals remain in the study area for the duration of the study.

It was originally hypothesised that species might show specific responses to the effects of marking and handling on initial capture compared with release after subsequent recaptures, in terms of the distance flown upon release. When the mean distance flown upon release after first time capture (when handling time was longer) was compared with the mean distances flown on subsequent capture events, most species showed no significant difference. Either a) there is no handling effect, b) there is a handling effect but the distance flown upon release is not a good measure of this, c) there is a handling effect and distance flown upon release is a good measure of this, but not revealed due to inaccuracy in distance measurement or d) no relationship found as distance flown is simply distance to the nearest appropriate alighting surface rather than in response to handling time (e.g. *Cissia* species tended to alight on sapling leaves 0.5 m off the forest floor; *Opsiphanes*, *Colobura*, *Temenis*, *Archaeoprepona*, *Prepona*, *Memphis* and *Caligo* species tended to alight on tree trunks and *Morpho peleides* tended to alight on vegetation 1-2 m off the forest floor, *personal observation*).

A highly significant positive relationship was found between forewing length and distance flown for new captures (of all individuals of all species encountered) and recaptures (r^2=0.461, F=560.14, p<0.0001 for new captures and r^2=0.412, F=165.4, p<0.0001). In a study on *Heliconius erato* butterflies, forewing length was found to

correlate significantly with the movement distances of pupal released individuals, but not with field captured ones (Mallet 1986). Mallet found that only 11 % of the variation was explained by the regression of movement distance on winglength and concluded that winglength was a poor predictor of dispersal distance in this species (Mallet 1986). In a study on predation and flight morphology in Neotropical rainforest butterflies (Chai and Srygley 1990), it was found that the chance for a butterfly to escape from a bird's (rufous-tailed jacamar) attack, was best predicted by the forewing length, thoracic width and relative wing area of that butterfly (r^2=0.61), using stepwise regression analysis (Chai and Srygley 1990).

In conclusion, this study has shown, that even with such a simple and relatively small grid of fruit traps (relative to the size of forest habitat), estimates of residency time, longevity and population size have been possible, which appear to reflect the results of the few other studies on Neotropical forest butterfly species.

Chapter 7

Community structure of *Cissia* butterflies

"Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare ?" Charles Darwin (1859).

7.1. Introduction

This Chapter explores the relative abundance of species in the *Cissia* group (Singer and Ehrlich 1993) of butterflies, within and between different habitats, studies and sampling methods. This assemblage was investigated using abundance data from four studies; i) walk-and-count in southern Trinidad (present study in Ch.3 and other data collected in 1995 but not previously used), ii) fruit trapping in southern Trinidad (present study, Chs.4 and 5), iii) walk-and-count in northern Trinidad (Singer and Ehrlich 1993) and iv) fruit trapping in Costa Rica (Daily and Ehrlich 1995).

A positive relationship has been demonstrated between local abundance and geographic distribution amongst ecologically similar species (Bock and Ricklefs 1983, Hanski 1982). It has been found that when closely related plants of the same life-form or animals of the same guild are compared, those species that have the highest local population densities tend to inhabit a greater fraction of the sample sites within a region and to have wider geographic ranges (Brown 1984, Gaston and Lawton 1988, Hanski 1982). Species that are rare also appear to have restricted ranges.

For Hanski these findings resulted in his 'core-satellite hypothesis' where he describes 'core' species as being locally common and widespread in distribution and 'satellite' species as being rare and restricted in distribution (Hanski 1982). Brown (1984) described a species abundance relationship in terms of the normal probability distribution curve where population density is highest near the centre of a species range

and declines towards the boundaries. "For each species there should be one most favourable site where population density should be greatest because the combination of environmental variables most closely corresponds to the requirements of the species. If spatial variation in the environment is autocorrelated, then with increasing distance from this site the environment will become progressively more different, niche requirements of the species will be met less frequently, and abundance will decline. There will be a decreasing number of local sites where individuals can occur at all, and even within these patches population density will tend to be lower because resources are scarce and/or conditions approach the limits that can be tolerated" (Brown 1984).

This positive abundance: distribution relationship has been shown to fit for many species groups including soil mites in Finland (Hanski 1982), scarab beetles in Sarawak (Hanski 1982), finch species in North America (Bock and Ricklefs 1983), diurnal birds of prey in North America (Brown 1984) and prairie plants in Kansas, North America (Gotelli and Simberloff 1987).

Aspects of community structure and the form of the abundance: distribution relationship were investigated for the *Cissia* group of butterflies. The *Cissia* group was chosen for several reasons. The species of the group are ecologically similar, sharing similar larval foodplants, the group is widespread across a range of habitats, found in all Neotropical communities and is relatively species rich.

The main objectives of the work described in this Chapter were to investigate:

1) aspects of the community structure of the *Cissia* group (Nymphalidae: Satyrinae), using data from studies undertaken in this thesis, comparing the findings with data from other sources.

2) the relationship between local abundance and the number of sites occupied, where a number of habitat sites have been sampled in a region in the course of undertaking the

study.

3) the relationship between local abundance and geographic range size for species in the *Cissia* group.

4) the predicted adverse effect of forest disturbance on restricted range species.

7.2. Methods

The *Cissia* relative abundance data come from walk-and-count and fruit trap data. The walk-and-count data come from nine samples undertaken in four habitats in 1994 (two undisturbed and two disturbed forest habitats, Ch.3), and in five habitats in 1995 (Trinity Hills (TH) undisturbed forest, TH disturbed forest, open grass between TH forest blocks, Guayaguayare (G) disturbed forest and G disturbed forest edge). The forest habitats TH 1994 and 1995 and G disturbed forest 1994 and 1995, are the same forest habitat transects sampled at the start of subsequent wet seasons, with different sampling effort. Walk-and-count data on *Cissia* species collected in ten habitats in northern Trinidad between 1970 and 1974 are also investigated (Singer and Ehrlich 1993).

The fruit trap data were collected in nine periods of sampling in seven forest habitats (two undisturbed and two disturbed forest habitats, Ch.3, two further periods of sampling in one of these undisturbed forest habitats, Ch.4, and three selectively logged forest habitats logged 0, 5 and 30 years previously, Ch.5). Fruit trap data from eight habitats in Costa Rica in 1993 and 1994 are also investigated (Daily and Ehrlich 1995).

7.2.1. Relative abundance and number of sites occupied

The relative abundance of each *Cissia* species in a particular sample was calculated. The relative abundance of the most dominant species is referred to as the Berger-Parker Dominance index value (d) (Southwood 1978), and was used as a measure of dominance of each *Cissia* assemblage.

Mean relative abundance values of each species over the number of samples in each study were also calculated and compared between studies.

Natural logarithm of mean relative abundance per site occupied was plotted against the

fraction of sites occupied. Analysis was carried out to see if these two variables were correlated.

7.2.2. Geographic range size and local abundance

The abundance: distribution relationship was then explored at a larger geographic scale for the butterfly abundance data collected in Trinidad. The relationship of the natural log of mean relative abundance per site occupied for each *Cissia* species in the present walk-and-count and fruit trapping studies, was investigated with respect to geographic range size estimates of each species. Geographic ranges were taken from accounts of species occurrence in published sources (D'Abrera 1981, D'Abrera 1984, D'Abrera 1987, D'Abrera 1987, D'Abrera 1988, D'Abrera 1994, DeVries 1987) and confirmed from BMNH collections.

The first categorisation of a species' geographic range size was either as (1) restricted (occur in some or all of Trinidad, Venezuela, Guianas and Amazonas) or (2) widespread (Wood and Gillman 1998). The abundance: distribution relationship was investigated for significance using a one-way ANOVA.

The second estimate was obtained by summing the areas of countries (Collins 1991) in which the species were found (Appendix B.1), and the third estimate used estimates of the actual habitat in which sampling took place, in this case lowland moist rainforest (Harcourt and Sayer 1996). The relationship of local abundance and these latter two geographic range size estimates was explored for significance using linear regression.

7.3. Results

7.3.1. Relative abundance and number of sites occupied

Walk-and-count sampling of the *Cissia* assemblage in Trinidad in 1994 and 1995, revealed that assemblages were dominated by *C. hermes* and *C. penelope* (Table 7.1). Over the nine habitats (seven habitats with two habitats sampled twice) it was found that *C. hermes* was the most abundant species in six habitats, with *C. penelope* being the second most abundant species, and in the other three habitats *C. penelope* was the most abundant species with *C. hermes* being the second most abundant species. The other nine species in the *Cissia* assemblage were found at lower mean relative abundance, *C. libye*, *C. hesione*, *C. cephus*, *C. myncea* and *C. arnaea* ranging from 0.083-0.045 and *C. renata*, *C. junia*, *C. terrestris* and *C. themis* ranging between 0.019-0.008 (Table 7.5)

The same *Cissia* species were encountered through fruit trapping, with the addition of *C. brixiola* (Table 7.2). Seven out of the nine habitats sampled were dominated by *C. penelope*, with several species being second most abundant (*C. hermes*, *C. hesione*, *C. myncea*, *C. terrestris*, *C. junia* and *C. cephus*). The other two habitats were dominated by *C. arnaea*, with *C. penelope* being second most abundant. These two habitats were the selectively logged forest habitats, one logged 5 and the other 30 years previously (Table 7.2). Mean relative abundance over the nine habitats revealed that *C. penelope* was most abundant, *C. arnaea* second most, with *C. hesione*, *C. hermes*, *C. junia* and *C. myncea* ranging in mean relative abundance from 0.095-0.042 and *C. terrestris*, *C. libye*, *C. cephus*, *C. renata*, *C. themis* and *C. brixiola* from 0.02-0.003 (Table 7.5).

In the other walk-and-count study (Singer and Ehrlich 1993), the most abundant species in five out of ten habitats was *C. hermes*, sharing this dominance with *C. erichto* in one habitat and *C. penelope* in another. *C. penelope* was most abundant in two further habitats, *C. myncea* and *C. hesione* the most abundant in one habitat each,

and *C. arnaea* and *C. junia* co-dominant in one habitat (Table 7.3). In Daily and Ehrlich's (1996) fruit trapping study, one *Cissia* species, *C. satyrina*, was very abundant in seven out of eight habitats, and in one habitat was equally most abundant with *C. arnaea* (Table 7.4).

Berger-Parker Dominance Index values varied from 0.32-0.63 and 0.19-0.75 in the two walk-and-count studies and from 0.46-0.93 and 0.45-0.995 in the two fruit trapping studies (Tables 7.1-7.4).

Four *Cissia* species were found in all four studies. These were *C. hermes*, *C. hesione*, *C. renata* and *C. arnaea*. From comparison of mean relative abundance and corresponding ranking in each study, *C. hesione* was moderately abundant in all four studies and ranked 4th, 3rd, 5th and 5th (in the order the studies are placed in the columns in Table 7.5), whereas *C. renata* was generally less abundant, being ranked 8th , 10th, 7th, and 4th, respectively (Table 7.5). *C. hermes* was the most dominant species, in both walk-and-count studies, but ranked 4th and 7th in the two fruit trapping studies. *C. arnaea* was the second most abundant species in the two fruit trapping studies but only ranked 7th and 6th in the two walk-and-counts.

Table 7.1. A comparison of the relative abundance and abundance ranking (in bold in parentheses) of *Cissia* species encountered during walk-and-count sampling in nine habitats. The relative abundance of the most dominant species in each sample is equivalent to the Berger-Parker Dominance Index value and was highlighted in bold

Cissia species	TH 94 forest	P 94 forest	G 94 disturbed forest	B4 94 disturbed forest	TH 95 forest	TH 95 disturbed forest	TH 95 open	G 95 disturbed forest	G 95 disturbed forest edge
penelope	0.103 (2=)	0.167 (2=)	0.258 (2)	**0.542 (1)**	0.286 (2)	**0.530 (1)**	0.286 (2)	**0.394 (1)**	0.253 (2)
hermes	**0.629 (1)**	**0.5 (1)**	**0.323 (1)**	0.232 (2)	**0.459 (1)**	0.317 (2)	**0.626 (1)**	0.309 (2)	**0.484 (1)**
hesione	0.035 (5)	-	0.226 (3)	0.062 (4)	0.031 (5)	0.027 (5)	-	0.085 (4)	0.074 (4)
myncea	-	-	0.048 (5)	-	0.020 (6)	0.060 (3=)	-	0.117 (3)	0.035 (6)
terrestris	-	-	-	0.006 (7=)	-	-	-	0.021 (6)	0.004 (9)
themis	-	-	-	-	-	0.005 (6)	-	0.011 (7=)	0.007 (8)
renata	-	-	-	-	0.010 (7=)	-	0.005 (4)	-	0.042 (5)
libye	-	0.167 (2=)	0.065 (4)	0.023 (6)	0.133 (3)	0.060 (3=)	0.083 (3)	0.053 (5)	0.081 (3)
arnaea	0.103 (2=)	0.083 (4=)	0.032 (6=)	0.057 (5)	0.010 (7=)	-	-	0.011 (7=)	0.021 (7)
junia	0.017 (6)	-	0.032 (6=)	0.006 (7=)	0.010 (7=)	-	-	-	-
cephus	0.069 (4)	0.083 (4=)	0.016 (8)	0.073 (3)	0.041 (4)	-	-	-	-

Table 7.2. A comparison of the relative abundance and abundance ranking (in bold in parentheses) of *Cissia* species from fruit trap sampling in nine habitats. The relative abundance of the most dominant species in each sample is equivalent to the Berger-Parker Dominance Index value and was highlighted in bold

Cissia species	TH 94 forest	P 94 forest	G 94 disturbed forest	B4 94 disturbed forest (2)	TH 95 forest study 1	TH 95 forest study 2	B6 96 forest (1 year)	B1 96 forest (5 years)	B7 96 forest (30 years)
penelope	**0.896 (1)**	**0.833 (1)**	**0.739 (1)**	**0.667 (1)**	**0.748 (1)**	**0.824 (1)**	**0.462 (1)**	0.233 (2)	0.018 (2=)
hermes	0.021 (3=)	-	0.087 (2=)	0.042 (4)	0.123 (2)	0.091 (2)	0.128 (3)	-	
hesione	0.063 (2)	0.167 (2)	0.087 (2=)	0.083 (3)	0.044 (3)	0.036 (3)	0.179 (2)	0.100 (3)	
myncea	0.021 (3=)	-	0.044 (4)	-	0.032 (4)	0.032 (4)	0.077 (5)	0.067 (4)	0.018 (2=)
terrestris	-	-	0.029 (5)	-	0.010 (6)	0.002 (8)	0.026 (6=)	0.033 (5)	0.018 (2=)
themis	-	-	-	-	-	0.003 (7)	-	-	
renata	-	-	-	-	0.006 (7)	0.005 (6)	-	-	
libye	-	-	-	-	0.003 (8=)	0.001 (9=)	0.026 (6=)	-	
amaea	-	-	-	-	0.025 (5)	0.006 (5)	0.103 (4)	**0.567 (1)**	**0.930 (1)**
junia	-	-	0.015 (6)	0.208 (2)	0.003 (8=)	-	-	-	
cephus	-	-	-	-	0.003 (8=)	0.001 (9=)	-	-	0.018 (2=)
brixiola	-	-	-		0.003 (8=)	-	-	-	

Table 7.3. A comparison of the relative abundance and abundance ranking (in bold in parentheses) of *Cissia* species encountered during walk-and-count sampling in ten habitats (data from Singer, 1996). The relative abundance of the most dominant species in each sample is equivalent to the Berger-Parker Dominance Index value and was highlighted in bold

Cissia species	Trace	Trace plantation	Guanapo	Dump 1	Dump 2	Cave	P.O.S.1	P.O.S.2	P.O.S.3	St. Ann's
palladia	0.008 (**8**)	-	-	-	-	-	-	-	-	-
terrestris	-	0.021 (**7**=)	0.013 (**6**=)	-	-	-	0.077 (**4**)	0.058 (**5**)	0.032 (**6**=)	0.043 (**7**=)
ocypete	-	-	-	-	-	-	-	0.032 (**8**)	0.065 (**4**=)	0.106 (**5**)
myncea	0.023 (**6**)	0.042 (**4**=)	0.013 (**6**=)	0.086 (**5**)	-	-	-	**0.269** (**1**)	0.161 (**3**)	0.128 (**4**)
hesione	0.030 (**4**)	0.250 (**2**)	0.078 (**4**)	0.029 (**7**=)	-	**0.615**(**1**)	-	0.224 (**2**)	-	0.085 (**6**)
libye	0.027 (**5**)	0.042 (**4**=)	0.033 (**5**)	0.029 (**7**=)	-	-	-	0.045 (**7**)	0.032 (**6**=)	0.043 (**7**=)
renata	0.103 (**2**)	0.188 (**3**)	0.118 (**3**)	0.143 (**4**)	-	-	0.115 (**3**)	-	0.065 (**4**=)	0.043 (**7**=)
hermes	**0.745** (**1**)	**0.313** (**1**)	0.359 (**2**)	0.286 (**2**)	**0.364**(**1**=)	-	**0.423**(**1**)	0.051 (**6**)	**0.323**(**1**=)	0.149 (**3**)
alcinoe	0.004 (**9**)	0.021 (**7**=)	-	-	0.045 (**4**)	0.077 (**3**)	-	0.006 (**10**)	-	0.021 (**10**)
themis	-	-	0.013 (**6**=)	0.057 (**6**)	-	-	-	-	-	-
penelope	0.015 (**7**)	-	**0.366** (**1**)	**0.343** (**1**)	-	-	0.385 (**2**)	0.013 (**9**)	**0.323**(**1**=)	-
amaea	0.046 (**3**)	0.125 (**6**)	0.007 (**9**)	-	-	0.308 (**2**)	-	0.135 (**4**)	-	**0.191**(**1**=)
junia	-	-	-	-	0.227 (**3**)	-	-	0.167 (**3**)	-	**0.191**(**1**=)
erichto	-	-	-	0.171 (**3**)	**0.364**(**1**=)	-	-	-	-	-

Table 7.4. A comparison of the relative abundance and abundance ranking (in bold in parentheses) of *Cissia* species encountered during fruit trapping in ten habitats (data from Daily and Ehrlich, 1996). The relative abundance of the most dominant species in each sample is equivalent to the Berger-Parker Dominance Index value and was highlighted in bold

Cissia species	Las Cruces 93 & 94	Cascada 93 & 94	Ridge Rd 93 & 94	Vaca Vaca 93 & 94	U.Gamboa 93 & 94	L.Gamboa 93 & 94	Lab slope 93 & 94	Lab stream 93 & 94
satyrina	**0.729 (1)**	**0.453 (1=)**	**0.994 (1)**	**0.995 (1)**	**0.994 (1)**	**0.953 (1)**	**0.876 (1)**	**0.964 (1)**
arnaea	0.097 (2)	0.453 (1=)	-	-	-	0.028 (2)	-	-
gigas	0.014 (6)	-	-	-	0.006 (2)	0.013 (3)	0.015 (5=)	0.036 (2)
hermes	0.028 (5)	-	-	-	-	-	0.019 (4)	-
hesione	0.076 (3)	0.047 (3=)	0.006 (2)	0.005 (2)	-	-	0.035 (3)	-
metaleuca	0.056 (4)	-	-	-	-	0.007 (4)	-	-
polyphemus	-	-	-	-	-	-	0.015 (5=)	-
renata	-	-	-	-	-	-	0.039 (2)	-
Cissia sp?	-	0.047 (3=)	-	-	-	-	-	-

Table 7.5. Ranking of *Cissia* species using mean relative abundance per site occupied within each of the four studies.

	W-and-count		Fruit trapping		W-and-count		Fruit trapping	
Mean Rank	**South Trinidad 94-95**		**South Trinidad 94-96**		**North Trinidad 70-74 Singer (1993)**		**Costa Rica 93-94 Daily & Ehrlich (1995)**	
1	*hermes*	0.431	*penelope*	0.609	*hermes*	0.335	*satyrina*	0.870
2	*penelope*	0.313	*amaea*	0.326	*erichto*	0.268	*amaea*	0.193
3	*libye*	0.083	*hesione*	0.095	*penelope*	0.241	*Cissia* sp?	0.047
4	*hesione*	0.077	*hermes*	0.082	*junia*	0.195	*renata*	0.039
5	*cephus*	0.056	*junia*	0.075	*hesione*	0.187	*hesione*	0.034
6	*myncea*	0.056	*myncea*	0.042	*amaea*	0.135	*metaleuca*	0.032
7	*amaea*	0.045	*terrestris*	0.020	*renata*	0.111	*hermes*	0.024
8	*renata*	0.019	*libye*	0.010	*myncea*	0.103	*gigas*	0.017
9	*junia*	0.016	*cephus*	0.008	*ocypete*	0.068	*polyphemus*	0.015
10	*terrestris*	0.010	*renata*	0.006	*terrestris*	0.041	-	-
11	*themis*	0.008	*themis= brixiola*	0.003	*libye*	0.036	-	-
12	-	-	-	-	*themis*	0.035	-	-
13	-	-	-	-	*alcinoe*	0.029	-	-
14	-	-	-	-	*palladia*	0.008	-	-

A significant positive relationship was found between the natural log of mean relative abundance of *Cissia* species per site occupied and the fraction of the total number of sites occupied for both the walk-and-count ($r=0.9025$, $df=9$, $p<0.01$) and fruit trapping ($r=0.763$, $df=10$, $p<0.01$) data sets (Fig. 7.1).

A similar positive relationship was found when natural log of mean relative abundance per site occupied against the fraction of the total number of sites occupied was plotted for Singer's (1993) and Daily & Ehrlich (1995) data sets (Fig. 7.2).

Figure 7.1. Natural log of mean relative abundance of *Cissia* species per site occupied against the fraction of the total number of sites occupied. Data from walk-and-count and fruit trapping undertaken in the present study

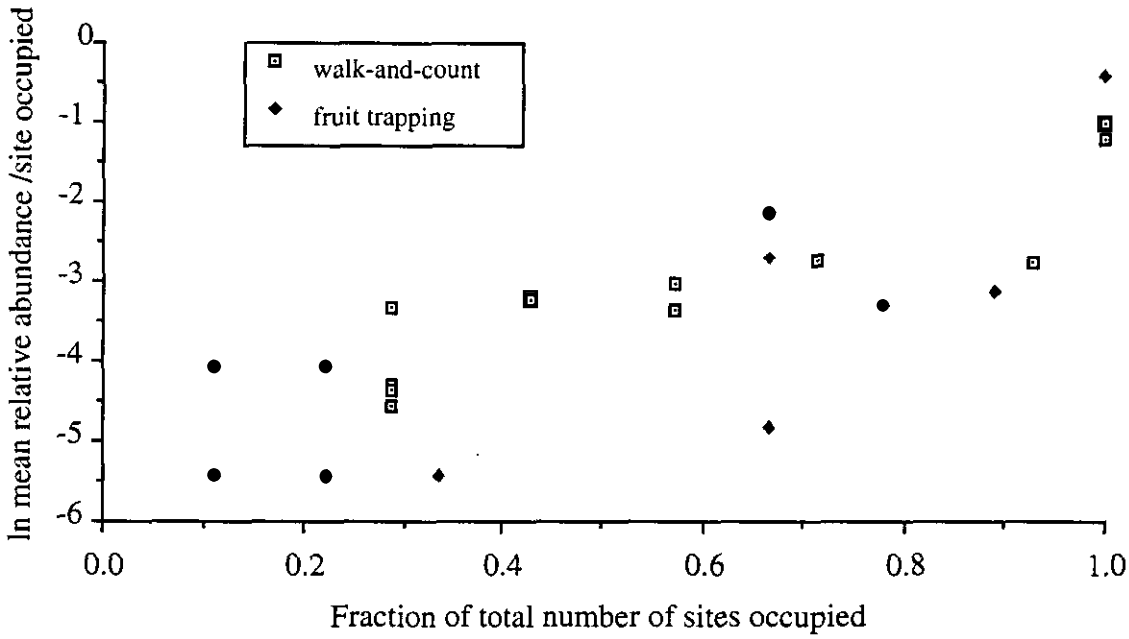
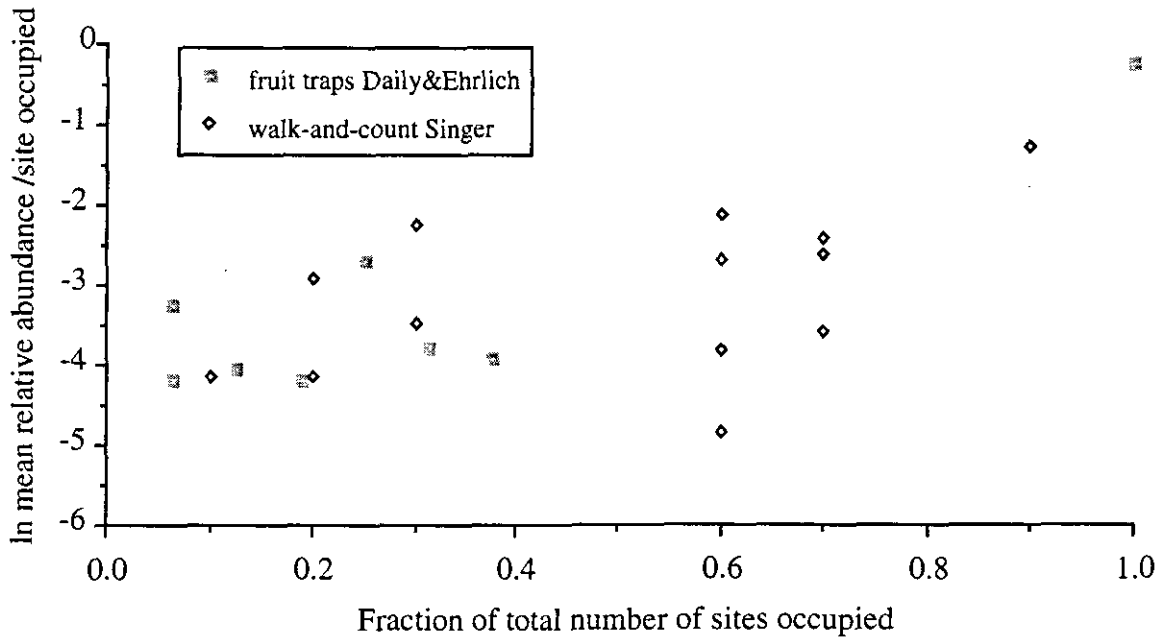


Figure 7.2. Natural log of the mean relative abundance per site occupied of*Cissia* species against the fraction of the total number of sites occupied. Data from (i) walk-and-count (Singer 1993) and (ii) fruit-trapping (Daily & Ehrlich 1995).



7.3.2. Geographic range size and local abundance

No significant relationship was found between local abundance measures and geographic range size when species' geographic range size was classified as either 1 (widely ranging) or 2 (restricted range), for either the walk-and-count (one-way ANOVA, F=0.129, df=1, p=0.728) or fruit trap data (one-way ANOVA, F=0.0013, df=1, p=0.972).

No significant relationships were found either for walk-and-count local abundance measures and geographic range size expressed in terms of land area (F=2.17, df=1, p=0.18, r^2=0.213, Fig. 7.3.a) or forest area (F=1.84, df=1, p=0.212, r^2=0.187, Fig. 7.3.b). No significant relationship was found either for the fruit trap local abundance estimates and land area (F=0.77, df=1, p=0.43, r^2=0.079, Fig. 7.4.a) or forest area (F=0.912, df=1, p=0.365, r^2=0.092, Fig. 7.4.b).

Table 7.6. Three classifications of *Cissia* species geographic range size and the local abundance (natural logarithm of mean relative abundance per site occupied) values used in the analyses of the abundance: distribution relationship.

	Local abundance		Geographic range size		
***Cissia* species**	**walk-and-count**	**fruit traps**	**1 or 2**	**Land area**	**Forest area**
penelope	-1.191	-0.396	2	3,827,965	3,411,810
hermes	-0.989	-2.137	1	17,855,314	8,667,860
hesione	-2.718	-3.124	1	11,205,575	8,667,860
myncea	-3.043	-3.307	2	3,998,941	2,731,330
terrestris	-4.290	-4.833	2	3,827,965	3,411,810
palladia	-	-	1	14,106,951	8,110,250
themis (=similis= urdina?)	-3.321	-4.052	1	?	?
renata	-2.769	-4.052	1	16,279,481	8,667,860
ocypete	-	-	2	3,827,965	3,411,810
erichto	-	-	2?	8,289,829	6,153,920
celmis	-	-	2?	5,077,955	?
cephus	-3.231	-5.439	2	3,827,965	3,411,810
junia	-4.351	-5.439	2	2,136,663	1,413,360
libye	-2.769	-5.439	1	8,339,080	6,070,030
arnaea	-3.358	-2.687	1	6,166,550	5,102,160
brixiola (=brixius?)	-	-5.439	2	3,366,111	2,408,390
alcinoe	-	-	2?	?	?

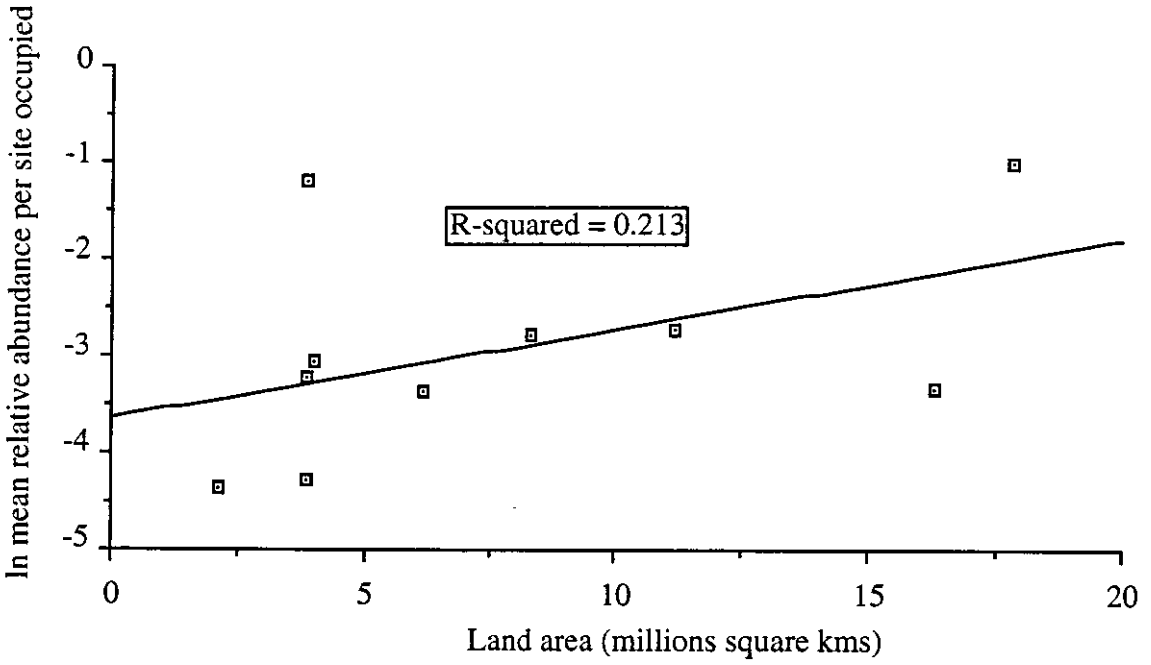


Figure. 7.3.a. Natural log of mean relative abundance per site occupied from walk-and-count data against geographic range size (land area)

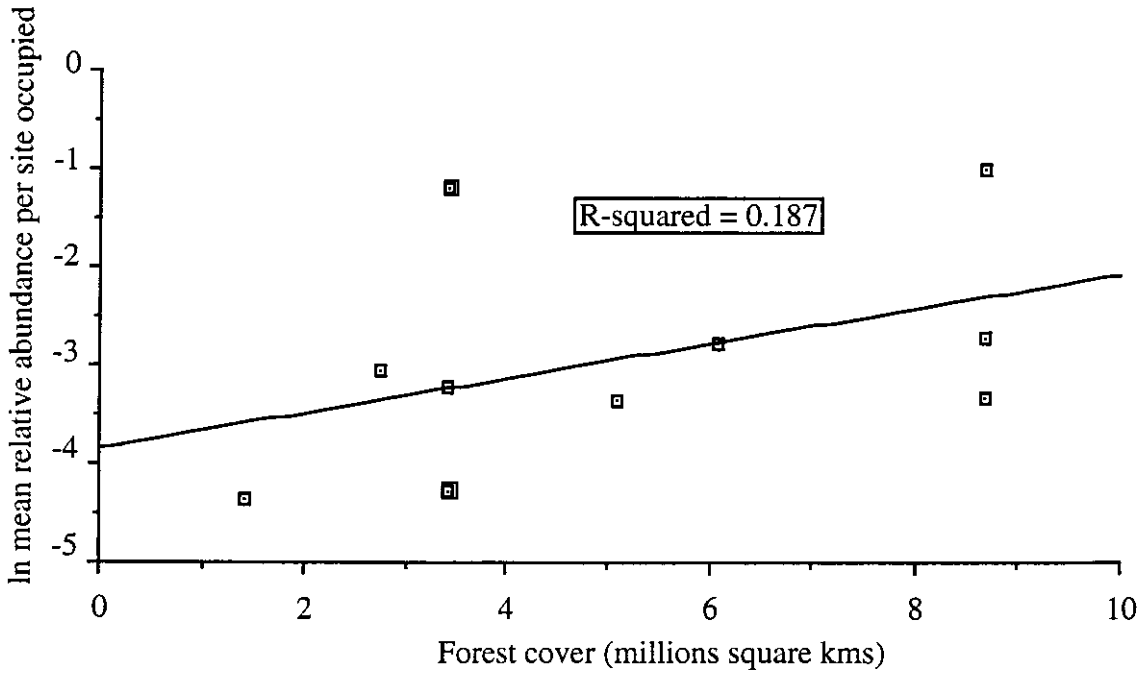


Figure 7.3.b. Natural log of the mean relative abundance per site occupied from walk-and-count data against geographic range size (forest cover)

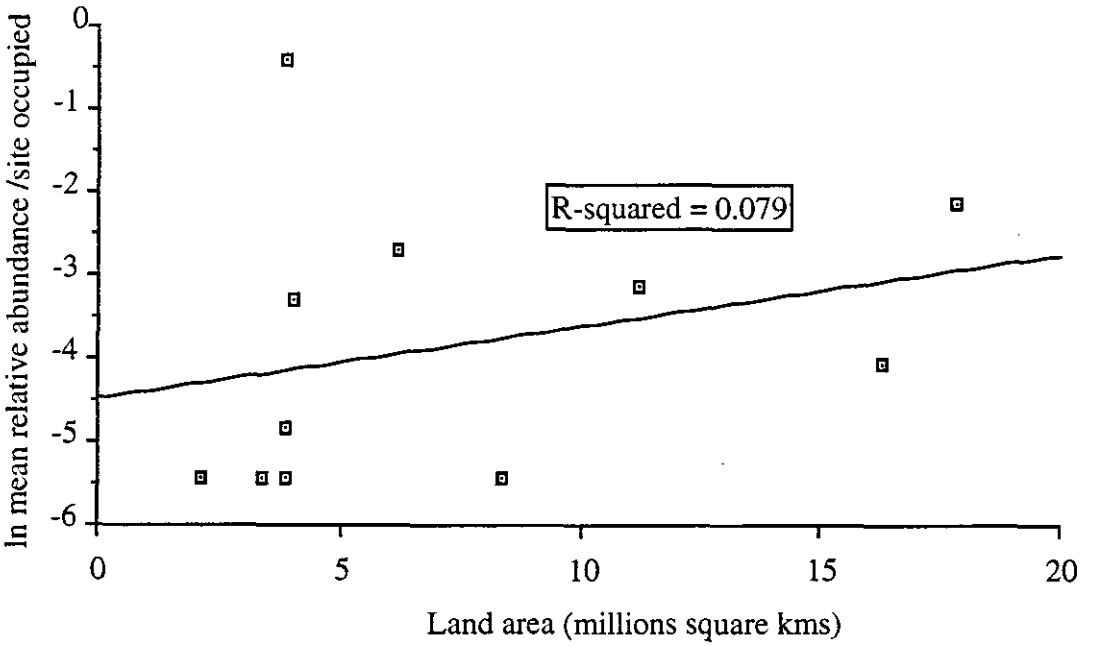


Figure 7.4.a. Natural log of mean relative abundance per site occupied from fruit trap data against geographic range size (land area)

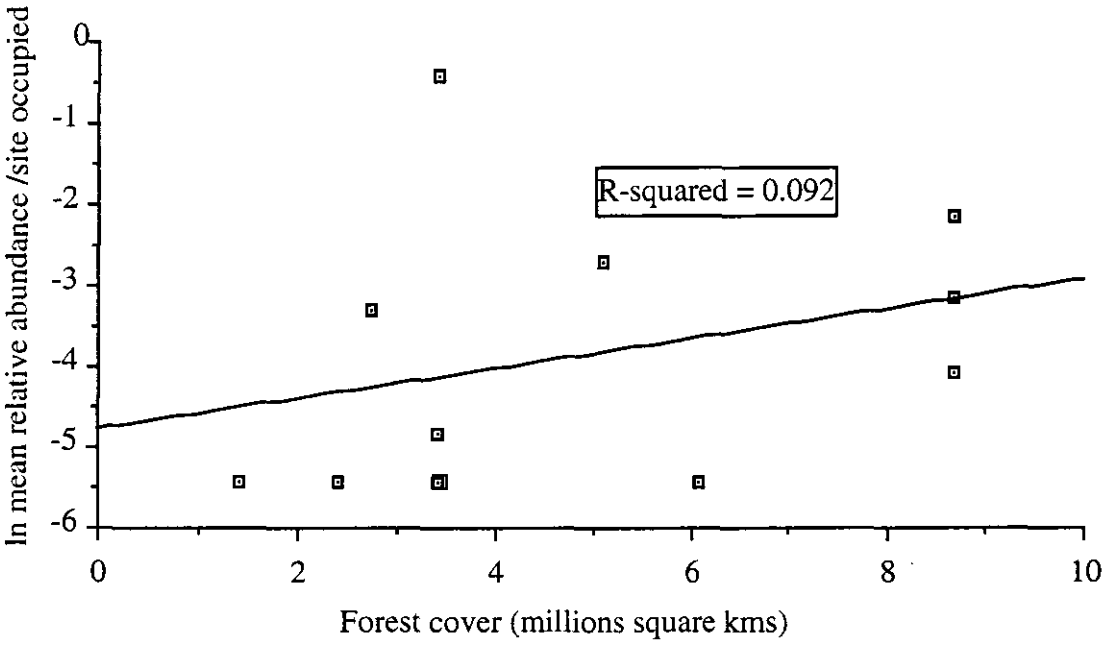


Figure 7.4.b. Natural log of mean relative abundance per site occupied from fruit trap data against geographic range size (forest cover)

7.4. Discussion

The significance of result interpretation using two sampling methods was clearly demonstrated here (also shown in Ch.3). From walk-and-count data, *C. hermes* was found to be the most abundant and *C. penelope* the second most abundant species. From fruit trapping, however, *C. penelope* was found to be most abundant, *C. arnaea* second and *C. hermes* fourth. Also, whereas *C. libye* was ranked third most abundant on average in the walk-and-count studies with a mean relative abundance of 0.083, it was ranked 8th from fruit trapping with a mean relative abundance of 0.01. Different result interpretation through the concurrent use of two sampling methods was reiterated for *Cissia arnaea.* From the two fruit trapping studies (present study and Daily & Ehrlich 1995), *C. arnaea* was the second most abundant *Cissia* species. From the two walk-and-count studies (present study and Singer 1993), however, *C. arnaea* was ranked 7th and 8th most abundant, respectively. It is possible that this difference in relative abundance of the same species using two sampling methods is due to the conspicuousness of the males (bright blue) or inconspicuousness of the females (brown). Positive identification of this species in walk-and-count sampling would probably rely on spotting the conspicuous males, with females being missed and therefore the species being under represented using this sampling method.

The converse pattern of differences between sampling methods was found for both *C. hermes* and *C. libye*, which were encountered relatively frequently in walk-and-count sampling but appeared infrequently in fruit traps. *C. hermes* is the only *Cissia* species which has been observed feeding on flower nectar, *Lantana camara* (*personal observation*), and so perhaps this species feeds on a range of adult resources, of which fruit is one, whereas other species feed exclusively on fruit. Such a non-exclusive fruit-feeder would therefore be under-represented by fruit trapping.

As reported in many other studies in the literature, there is often a positive relationship between mean abundance in occupied sites and the number of sites occupied. This

extends to the larger spatial scale of geographic distribution and local abundance. At least eight mechanisms have been proposed to explain this relationship, invoking sampling artefacts (locally rare species being more dfficult to detect than common ones and hence appear at fewer sites, distorting results), phylogenetic non-independence, range position, resource breadth, resource availability, density-dependent habitat selection, metapopulation dynamics and vital rates (Gaston *et al.* 1998).

From a recent collation of published studies (Gaston 1996), significant positive relationships were found in 71 cases compared with only five reporting a significant negative relationship. Non-significant relationships were reported in 13 studies (Gaston 1996). From analyses for birds at sites in Britain, Gaston and Lawton (1990) proposed that the form of the relationship between species' local abundance and regional distribution is dependent upon the match between reference habitat in which abundance is measured, and all habitats in the area over which distributions are measured. When reference habitat is relatively common, a positive abundance: distribution relationship is found. When unusual, no clear pattern is found, and when reference habitat is rare, a negative relationship is observed (Gaston and Lawton 1990). In the present study, the 'reference' habitat is relatively abundant (see Table 7.6), and the relationships between local abundance and geographic range size were positive, although not significant.

It is felt that the largest inaccuracies in the study of these abundance: distribution relationships lie in the estimation of the geographic range size. Accounts of species geographic range distributions tend to be of the nature, 'Mexico to southern Brazil' (D'Abrera 1988), for *Cissia renata*, for example. From a map of Central and South America one could assume that the distribution of *C. renata* ranged from Mexico and through Central America, to Colombia, Venezuela, the Guianas, Amazonas and southern Brazil. However, whether or not *C. renata* is found in Ecuador, Peru, Bolivia and Paraguay would be unclear. DeVries (1987) describes the geographic range of *C. renata* as 'Mexico to Ecuador'. From these two published accounts of the geographic range of *C. renata* it is likely that this species ranges from Mexico through Central

America, Colombia, Venezuela, Guianas, Amazonas to southern Brazil and Ecuador. Accuracy of geographic ranges was improved with research from a number of published sources and museum collections (British Museum of Natural History). The geographic range distributions of species are shown in Appendix B.1).

The land area interpretation of geographic range size is undoubtedly an over-estimate, as it incorrectly assumes species occur throughout a country's range of heterogeneous habitats, both natural and unnatural. The ecological range of a species takes into account the preferred habitats of species. Ecological range size estimates are the sum of species' appropriate habitat areas from the countries in which it has been recorded. This produces a more ecologically appropriate geographic range size estimate, but as Gaston has noted, land area and ecological range size estimates are often strongly related (Gaston 1994). This again is likely to be an over-estimate of a species' true geographic range size, as it is unlikely a species will occur in all pockets of suitable habitat. Increasing the accuracy of ecological ranges could be achieved through the plotting of species records using GIS and extracting 'extents of occurrence' estimates of geographic range size (McGowan and Gillman 1997). If extensive and detailed species locality data were available across a species' geographic range, 'areas of occupancy' estimates could be calculated, which represent the actual distribution of a species within the extents of occurence range. Unfortunately, these data do not exist.

Forest disturbance has been predicted to affect restricted range species more adversely than widespread species (Thomas 1991). This was not found to be the case for several restricted range species in this study, however. As decribed in this Chapter, *C. penelope* was found in high abundance in Trinidad using both walk-and-count and fruit trapping, and has also been reported in great abundance in Ecuador (DeVries *et al.* 1997). Similarly, *Catoblepia berecynthia* and *Pierella hyalinus*, classified as restricted in this study, were also found as abundantly in disturbed as in undisturbed forest habitats. This may be a semantic issue concerning the definition of 'restricted' when applied to geographic range and the extent of 'disturbance' when applied to a forest. Other

workers have found species with more restricted geographic ranges being present only in closed canopy forest in Vietnam (Spitzer *et al.* 1997), and restricted range species being at highest density in undisturbed primary forest in Sumba, Indonesia (Hamer *et al.* 1997).

An aspect of geographic range size classification which has not been taken into account, is the current status or trend of species' geographic ranges in terms of range expansion and contraction. It may well be, for example, that *C. penelope* has been going through a period of geographic range expansion in the last 100 years, and so perhaps should now be considered a widespread species. The data to test this are not available, however.

Chapter 8. General discussion

Different aspects of the effects of tropical forest disturbance and fragmentation on butterflies, and in particular the fruit-feeding guild of butterflies, have been explored in preceding chapters of this thesis. The present study investigates responses of butterflies from entire habitat assemblages to individual species in light of aspects of forest disturbance and fragmentation, at a wide range of spatial scales. In this chapter I discuss and summarise the main results presented in this thesis, thereby evaluating their contribution to various areas of tropical butterfly and forest ecology.

8.1. Response to forest disturbance and forest recovery

Several taxonomic groups have been proposed as potential indicators of habitat disturbance including tiger beetles (Rodriguez, *et al.* 1998) and butterflies (Brown 1991; Hill, *et al.* 1995). The walk-and-count censuses carried out in South-East Trinidad revealed that butterfly species richness was greater in disturbed forest habitats, whereas fruit trapping revealed similar numbers of species in all habitats, although in contrast to walk-and-count, fewest species in the disturbed evergreen forest.

The butterfly assemblages encountered through walk-and-count surveys in the same disturbance level (ie. both disturbed or both undisturbed habitats in different forest types) showed greater similarity than between the disturbed and undisturbed habitat in the same forest type. This implies that within a region of forest, butterflies are characteristic of disturbance rather than forest vegetation type. This lends further weight to the belief that butterfly faunas can be used as bioindicators of disturbance.

When assemblages were compared between walk-and-count (forest understorey) and canopy fruit traps, high dissimilarity was evident between the two undisturbed habitats sampled (mean Dice association index value of 0.21) whereas similarity was much

greater between the disturbed habitats (mean association index value of 0.61). This suggests that the canopy of the disturbed forest habitats were too disturbed to maintain a distinct canopy fauna from an understorey one, whereas the undisturbed habitats do have a stratified butterfly assemblage. Vertical stratification in the fruit-feeding butterfly fauna has also been reported from Costa Rica (DeVries 1988).

In this study, the rate of fraction of species accumulated in a forest habitat was found to be useful in characterising a habitat relative to its level of disturbance (Ch. 3). It was found that in general, disturbed habitats had higher rates of species accumulation than undisturbed habitats. However, in stark contrast to the walk-and-count data which showed the highest species accumulation rate in the disturbed evergreen forest habitat, fruit trap data revealed that this same habitat had a significantly lower species accumulation rate compared with all other habitats. Only through the concurrent use of these two sampling methods was this difference between butterfly assemblages within the same habitat detected. With further work on a range of habitats differing in disturbance level, it is theoretically possible that threshold rates of butterfly species accumulation could be found which would indicate the recovery of a particular forest habitat type following disturbance, to a level characteristic of undisturbed habitats.

It seems likely that any conclusions about the extent of tropical forest disturbance which can be tolerated may be taxon-specific, a point also made by Margules *et al.* (1994). Termite species richness in southern Cameroon was found to be greatest in old secondary and plantation forest, followed closely by near primary forest, the least disturbed habitat, and lowest in two severely disturbed plots (Eggleton, *et al.* 1995). This enhancement in species richness at intermediate levels of disturbance (Connell 1978) is in contrast to the pattern observed with termite species in Sarawak (Collins 1980) and other invertebrate groups such as moth species in Malaysia (Holloway, *et al.* 1992) and scarab beetles in Manaus, Brazil (Klein 1989), where a decrease in species richness and species diversity was found as forest habitats became more disturbed and

fragmented. This pattern is also observed with bird species, where increased levels of disturbance and increased light levels one year after selective logging in French Guiana, resulted in an overall 27-33% decrease in species richness (Thiollay 1991). A reduction in both the number of understorey bird species and their abundance was also found by workers looking at the edge effects of forest fragmentation in Brazil (Lovejoy, *et al.* 1986) and in peninsular Malaysia (Johns 1986).

In this study (Ch.5), the abundance of particular butterfly species have proved useful as indicators of forest recovery following selective logging. Two fruit-feeding species were found to respond contrastingly to the process of forest recovery following logging, with respect to mean canopy openness. *Cissia arnaea* was found at low abundance immediately following logging and found to take between six and 30 years to attain high abundance levels. In contrast, *Colobura dirce* was found at greatest abundance immediately following logging and five years later, but was found at much lower abundance levels after 30 years of forest recovery (Ch. 5). Thirty years is currently the rotation cycle between logging events in the Periodic Block System in Trinidad. After further fruit trapping in blocks of forest logged between 5 and 30 years ago, the presence of butterfly species such as *C. arnaea* in high abundance and *Colobura dirce* in low abundance, could be used as an indicator of forest recovery following logging.

Certain other *Cissia* species were found in greater abundance in more open canopied forest localities and others in more closed ones (Ch. 5). *C. penelope* and *C. hermes* were found in greater abundance in recently opened gaps (Ch.5), to be distributed more abundantly at a forest edge than either 20 m or 40 m into the forest (Ch. 4) and were found to have crossed breaks of open ground between forest blocks (Ch.4). These two species feed on a suite of at least 11 grass and sedge species and have been classified as hostplant generalists (Singer and Ehrlich 1993). This is in contrast to *C. arnaea*, which is a hostplant specialist, feeding exclusively on one grass species, *Ichnanthus pallens* (Singer and Ehrlich 1993). *C. arnaea* was found to be more abundant in closed canopy

conditions (Ch. 5, noted above) and was not found to have crossed the open areas created by a road or gas-line (Ch.4). In light of this finding, future work should investigate the *Cissia* species group to elucidate whether hostplant specialists are more restricted to forest core habitats, compared with the generalist species, and hence more likely to avoid crossing habitat breaks and consequently be affected more adversely by forest disturbance and fragmentation.

Work in montane forest in northern Vietnam found that although butterfly species richness and diversity was higher in gaps, the conservation value of the closed canopy habitat lay in the presence of species with restricted ranges (Spitzer, *et al.* 1997). Similarly, work on birds in Malaysia (Wells 1988) found that fresh gaps large enough to expose the ground to full sun were avoided by all shade-layer species, with canopy species being less impeded. Two gaps of 0.5-1 ha took ten years to acquire their first shade-adapted birds. This avoidance of pioneer growth by these birds was thought to be due to sensitivity to high temperatures and a well known behavioural avoidance of bright light.

The results of this study suggest that butterflies may prove useful as indicators of forest disturbance both as an assemblage and as particular species. As this study only investigated the butterfly fauna, these results do not suggest that there may also be other suitable taxonomic groups as good or better than butterflies as indicators of forest disturbance. What the whole study suggests, however, is that in the case of Trinidad forest habitats, butterflies are a manageable taxonomic group, species being well-known and readily identifiable. Tiger beetles, widely cited as excellent indicator species (Pearson and Cassola 1992) and as indicators of disturbance (Rodriguez, *et al.* 1998) would not have been suitable in the present study, due to only four species being found in Trinidad.

8.2. Forest fragmentation effects

The largest single problem that causes conservation problems is habitat loss. Of the remaining areas, many have been disturbed or fragmented into smaller patches. In many tropical regions, rain forest is restricted to small (<100 ha) isolated fragments (Turner and Corlett 1996). Forest fragmentation results in potential barriers to movement, increased amounts of forest edge and higher numbers of small patches with associated increases in the likelihood of local extinction. Recent research has shown that a substantial number of forest species can persist for decades in fragmented forest, though large vertebrates are susceptible to habitat fragmentation (Turner and Corlett 1996).

The smaller the forest fragment, the higher the ratio of forest edge habitat to forest interior habitat. Several fruit feeding species were found to be horizontally stratified in their distribution from a forest edge to 40 m into forest. The two Satyrinae species, *Cissia penelope* and *C. hermes*, were found in greatest abundance at the forest edge and declined in abundance further into forest. The opposite pattern of horizontal stratification of highest abundance 40 m into the forest, declining in abundance to the forest edge, was observed for two species, *Morpho peleides* and *Colobura dirce*. Forest fragments will tend to lose forest-dependent species and gain forest-edge species. Forest fragments in Manaus, Brasil (Brown 1991) showed a dramatic increase in butterfly species richness in fragments with increased understorey light levels, such as internal forest clearings and fragments which were semi-isolated (increased proportion of edge habitat), compared with inside forest.

In this study, butterflies were found to respond differently to the potential barrier to dispersal of a break in the forest habitat. Some species were found to move preferentially along the forest edge whereas others moved deeper into the forest. Some species were found to cross breaks (~40 m) of open ground frequently whereas others

were found never to have crossed. Male euglossine bees have been found to be unable to cross breaks of open ground (100 m wide) in Amazonia (Powell and Powell 1987). The movements across breaks between forest blocks observed for five species in the present study, were not found to be significantly different from the number of individuals expected to cross, using the formula derived by Munguira and Thomas (1992). The seven other species recaptured crossing breaks were not tested for significance due to expected values of less than five. Several of the species not recaptured crossing breaks have been seen either crossing breaks (*Hamadryas feronia*, *C. libye* and either an *Archaeoprepona* or *Prepona* species), flying in one of the breaks (*Biblis hyperia* and an *Adelpha* species), or feeding in open areas (*Opsiphanes cassina* and *Historis acheronta*). Further sampling would increase the probability of recapturing individuals of these species crossing the breaks.

Workers in Spain (Baz and Garcia-Boyero 1995) discovered a significant correlation between butterfly species diversity and woodland area, diversity increasing as the area and patchiness of the fragment increased. Increased patchiness with increased forest fragment area was the result of decreases in certain structural variables of the habitats. Work on the effects of eucalyptus forest fragmentation on a scorpion *Cercophonius squama* and an amphipod in South-east Australia, discovered that the abundance of scorpions did not change significantly with fragmentation, whereas amphipod abundance decreased markedly (Margules, *et al.* 1994).

8.3. Population ecology of butterflies from fruit trap data

Uniquely marking individuals not only enables individuals to be tracked spatially through the environment, but also temporally. The time between first capture and last recapture of an individual is referred to as an individual's residency time and reflects the length of time an individual remains in the study area. If individuals are restricted to the study area, ie.the study area encapsulates the home range of the individual, then this may also be a reflection of the individual's longevity. Emigration, death or trap shyness are possible reasons for the loss of an individual from a fruit-trapping MRR study.

Trap shyness was suspected for both *Cissia hermes and C. libye* Individuals of both species were frequently observed on walk-and-count surveys in the study area but rarely caught in fruit traps. For example, 13 *C. libye* individuals were encountered in 321 minutes of walk-and-count transects in undisturbed semi-evergreen forest, compared with one individual after fruit trapping for 11,124 trap hours (18 traps x 618 hours). Over the same sampling periods in the same habitat, 106 *C. hermes* individuals were encountered undertaking walk-and-count sampling and 8 individuals in fruit traps. It is possible that fruit-feeding species differ in their likelihood of being caught in fruit traps, perhaps due to differences in diet breadth. Whereas some species may feed exclusively on fruits and hence would be over-represented by fruit trapping, many species also feed on a variety of other resources including fish, animal dung and urine, fungi and tree sap, which may under-represent these species in a fruit trapping exercise. The numbers of individuals encountered using walk-and-count and fruit trap sampling, with their different sampling efforts respectively of person-hours (time walked per person sampling) and trap-hours (time fruit traps baited and available for trapping) are not directly comparable. This is further complicated by the fact that whereas fruit trapping only enables those individuals which are foraging for food resources to be encountered (food resources which may be plentiful and / or more attractive elsewhere), walk-and-count methods allows individuals to be encountered undertaking the whole range of adult activities including feeding, basking, flying,

searching for ovipostion sites and ovipositing, searching and displaying for mates, mating and patrolling territories. It is not known how the movements and disributions described for fruit-feeding species in this study reflect natural daily or seasonal movements. A similar point has been made by Hill and colleagues (1995) with reference to the reported stratification of the fruit-feeding guild of butterflies (DeVries 1988), in that it is not known if this stratification remains when species are not feeding.

Nevertheless, residency rates and times, longevity and population sizes were estimated for several of the most abundant species captured in fruit traps. The lack of examples of similar population structure information for other tropical butterfly species (with the exception of the *Heliconius* group of butterflies) makes the possible problems associated with these estimates of secondary importance, as at least estimates have been made. *Cissia penelope* was estimated to have average residency times of 1.71 and 4.42 days in study 1 and 8.41 days in study 2, although one *C. penelope* individual was encountered over a 9.5 week period. The average residency times of *Morpho peleides* (male and female data combined) was 6.6 days in study 1 and 3.6 days in study 2 and males were found to have higher average residencies than females (12.0 days compared with 4.0 days in study 1 and 3.1 days compared with 2.4 days in study 2). The average residency times in the present study were of a similar order of magnitude to those found for temperate butterfly species, with few comparable data found in the literature for tropical butterfly species. The longest residency recorded for a *Morpho peleides* male in the present study was 31 days, which compares well with that reported in a Costa Rican forest fragment of 33 days (Young and Thomason 1974).

An overall *C. penelope* population size for study 1 was 563, with half-daily estimates ranging between 0 and 128. In study 2 the overall population size estimate over the duration of the study was 902, with daily estimates ranging between 30 and 800. *Morpho peleides* was found at much lower population sizes in both studies compared with *C. penelope*. In study 1, half-day population estimates ranged between 0 and 32, with a total population size estimate over the course of the study of 53. Over the course

of study 2 the overall *Morpho peleides* population size was estimated at 163, with half-day estimates ranging from 4 to 60.

It is realised that the movements described in this study are entirely dependent on the positioning of the fruit traps and the number and spacing of these traps are a limiting factor. A larger grid may well uncover the more subtle differences in the extent of movements between species. What this study has shown, however, is that even with such a simple and relatively small grid of fruit traps (relative to the size of forest habitat), important questions relating to horizontal stratification at a forest edge and whether species can cross a thin break in the forest, have begun to be answered.

8.4. Forest disturbance and the relationship between local abundance and geographic range size

Significant positive correlations were found between mean relative abundance of *Cissia* species per site occupied and the fraction of the total number of sites occupied. Positive, but not significant, relationships were also found between mean relative abundance and geographic range size in terms of land area and in terms of forest cover.

Butterfly species with narrow geographic ranges have been thought to be less able to make use of human-modified environments than more widely distributed species (Thomas 1991). Hence forest disturbance is more likely to affect endemic species adversely. Work on Sumba, Indonesia, reported that butterfly species occurring at the highest densities in secondary forests had wide geographic ranges and those at highest densities in undisturbed primary forest were restricted range species (Hamer, *et al.* 1997). As opposed to secondary forest in northern Vietnam, closed canopy habitat was found to contain species with restricted ranges (Spitzer, *et al.* 1997). However, more restricted range species such as *Cissia penelope*, *Catoblepia berecynthia* and *Pierella hyalinus* were not found to be adversely affected by forest disturbance at this level (Appendices B.1 & B.2). *C. penelope* was found in high abundance in this present

study using both walk-and-count and fruit trapping, and has also been reported in great abundance in Ecuador (DeVries, *et al.* 1997). Similarly, *Catoblepia berecynthia* and *Pierella hyalinus*, classified as restricted in this study, were also found as abundantly in disturbed as in undisturbed forest habitats. Unlike *C. penelope*, however, there were not other *Catoblepia* or *Pierella* species in Trinidad with which to compare the relationship of local abundance and geographic range size with. This may be a semantic issue concerning the definition of 'restricted' when applied to geographic range and the extent of 'disturbance' when applied to a forest.

As a whole, this study has shown that through the use of two butterfly sampling strategies, sometimes concurrently, species assemblages and particular species can reflect differences in forest disturbance. Occasionally the two sampling methods revealed contrasting results which enriched the findings compared to those found if only one or other of the sampling methods had been employed. Further work at larger spatial and temporal scales would hopefully reveal lifetime movements of many species, uncovering home-ranging behaviour or perhaps movements dictated by fruit abundance. Further MRR work across narrower and wider breaks in the forest, would aid in assessing the potential effects of future forest fragmentation. Finally, I hope that many others can experience the joy of chasing butterflies through tropical forests, and it remains possible throughout this next millenium.

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Appendix A

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The effects of disturbance on forest butterflies using two methods of sampling in Trinidad

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The butterfly assemblages of pairs of forest habitats, differing in disturbance level, within the Victoria Mayaro reserve of South-East Trinidad, are described using walk-and-count transects and canopy and understorey fruit traps. The concurrent use of these two butterfly censusing techniques, revealed major but conflicting differences in species accumulation rates under different disturbance conditions. The disturbed evergreen habitat had the significantly highest accumulation rate from walk-and-count data but the significantly lowest from fruit trap data. This reflects the specificity of much of the fruit-feeding guild for closed canopy forest. Disturbed habitats were found to lack a distinct canopy fauna. These results are discussed in light of the intermediate disturbance hypothesis. Within a region of forest, butterflies were found to be more characteristic of a disturbance level than of a particular forest type, lending weight to the belief that butterfly faunas can be used as bioindicators of forest disturbance. Several restricted geographic range species were not adversely affected by forest disturbance, at these levels of disturbance. The butterfly censuses in this study suggest that the optimal strategy for safeguarding butterfly species richness under natural forest management regimes would be to maintain a mosaic of habitats that included areas of undisturbed primary forest and a network of other forest patches, that varied in management regime and level of disturbance.

Keywords: butterflies; tropical forest; disturbance; selective logging; conservation.

Introduction

Tropical forest ecosystems are under threat across the world as anthropogenic pressures increase. Squatting, shifting cultivation, hunting and enhanced levels of timber extraction are some of the most widely seen effects of this increased pressure. A global research priority is an assessment of the effects of this forest disturbance on wildlife and a determination of the value of these degraded forests to conservation.

Butterflies have been suggested as potentially excellent environmental indicators in temperate and tropical regions (Gilbert, 1984; Brown, 1991; Kremen, 1992). The dependence of the larval stage on a specific host plant, combined with the adults' roles as pollinators for other plants, link butterflies closely to the diversity and health of their habitats (Ehrlich, 1984). Butterflies are also very sensitive to changes in temperature, humidity and light levels, parameters that are typically affected by habitat disturbance. Butterfly taxonomy is well known compared with other tropical insect groups and many species can be reliably identified in the field.

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This paper analyses the composition of butterfly assemblages in two pairs of forest habitats in the Victoria Mayaro Reserve in South-East Trinidad (Fig. 1). Each pair of habitats comprised a disturbed and an undisturbed forest habitat. The use of fruit trapping techniques and walk-and-count butterfly censusing methods ensured sampling of a wide spectrum of the forest butterfly fauna (Sparrow, 1994) and allowed an investigation into the stratification of the butterfly assemblage.

Methods

Study sites

Trinidad is an ideal locality for the study of Neotropical butterflies, having broken away from continental South America ca. 10 000 years ago and containing a well documented fauna (Barcant, 1970). The island of Trinidad is roughly rectangular in shape measuring ca. 56 by 77 km (Fig. 1). Three mountain ranges traverse the island. The Southern Range consists of a series of low rolling hills extending along the south coast from Erin to Guayaguayare. Most of the hills in this range are only 60–90 m high, but in its eastern portion, the Trinity Hills rise to 300 m. Rainfall varies from between 1650 mm and 2500 mm per year. There are two seasons per year, a dry season extending from January to May, and a rainy season from May to December. Temperatures in any year rise to a maximum of 35°C and drop to a minimum of 15°C.

A large portion of the 52 000 hectare Victoria Mayaro Forest Reserve (Fig. 1) is evergreen seasonal forest dominated by *Mora excelsa* Benth. (Leguminosae), a tree species that can make up to 85–95% of the individuals forming the forest canopy (Clubbe and Jhilmit, 1992). Farther south, the forest becomes drier and semi-evergreen, dominated in the canopy by *Carapaguianensis* Aubl. (Meliaceae) and *Pentaclethra macroloba* (Willd.) Kuntze (Leguminosae).

Butterfly populations were investigated in these two forest types (Fig. 1). Pairs of habitats were chosen in each forest type on the basis of differing management histories which were likely to have resulted in different levels of disturbance. Each habitat in a pair was called disturbed or undisturbed. The undisturbed evergreen forest (1) had no known history of management, while the disturbed evergreen forest habitat (2) had recently been selectively logged. The undisturbed semi-evergreen forest was situated in the Trinity Hills Wildlife Sanctuary (3) while the disturbed semi-evergreen forest, 3 km away, was a disused cocoa plantation (4) (Fig. 1.). Disturbance in this case refers to the increase in the number of openings in the canopy caused by tree felling, and the subsequent disturbance of the understorey and ground layer caused by the treefall and extraction.

Butterfly census methods

Two methods of collecting butterfly abundance information were used in each of the four habitats. These were walk-and-count transects, and fruit traps placed in both the understorey and the canopy sited along the walk-and-count routes. Walk-and-count transects were carried out for four consecutive weeks whereas fruit trapping was carried out alternately for 1 week in the understorey and 1 week in the canopy over the same 4-week period (Table 1).

Within each habitat category, walk-and-count transect routes of 0.25 (disturbed semi-evergreen), 0.37 (undisturbed semi-evergreen), 0.42 (disturbed evergreen) and 0.55 km (undisturbed evergreen) were walked and mapped. The transects were intended to take

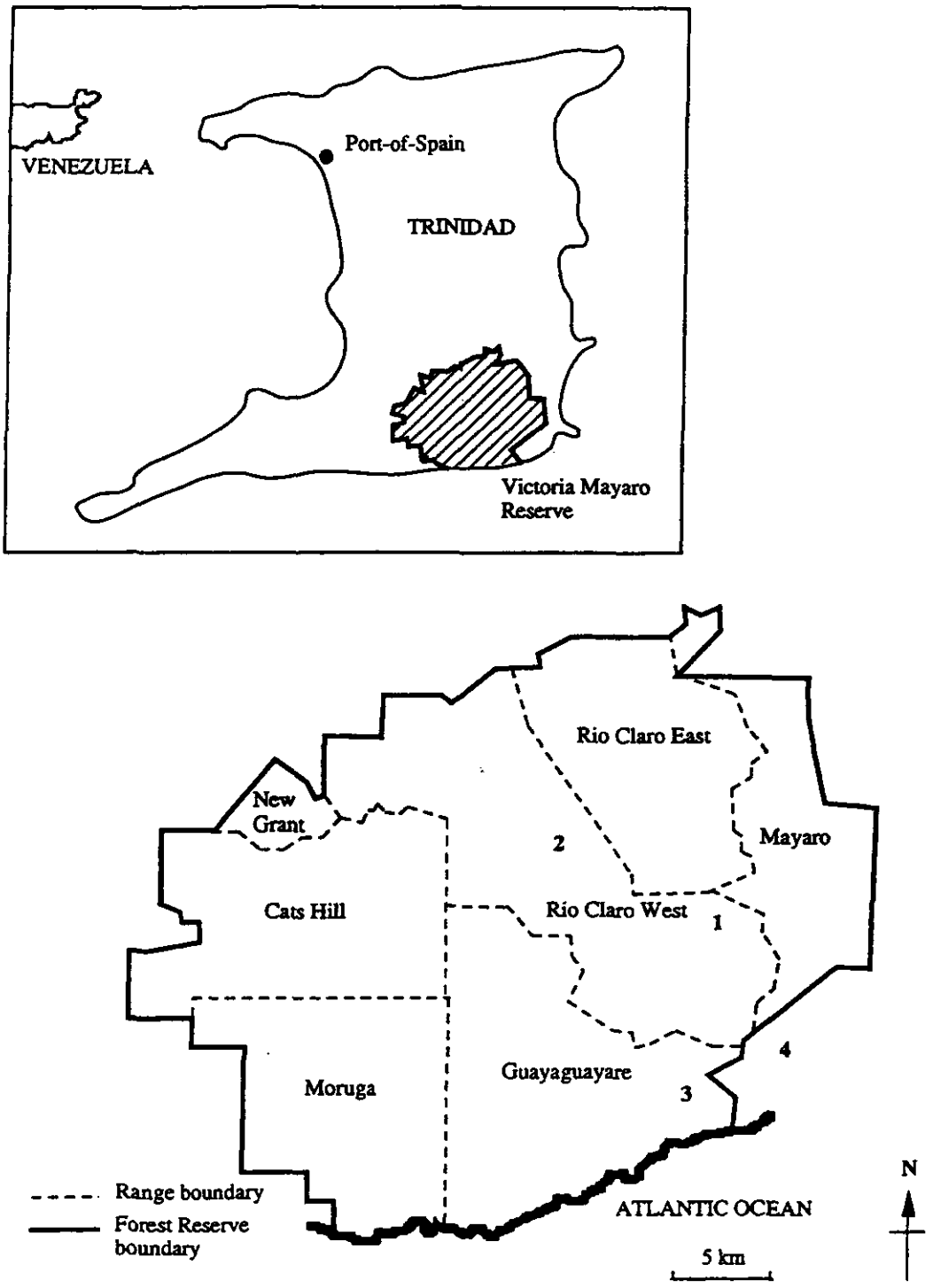


Figure 1. A map of Trinidad showing the Victoria Mayaro Reserve and the four forest habitats studied: evergreen undisturbed (1) and disturbed (2) forest and semi-evergreen undisturbed (3) and disturbed (4) forest.

Table 1. Sampling timetable: weeks when walk-and-count transects (——) , canopy fruit trapping (- - - -) and understorey fruit trapping (·····) , were carried out in each forest type in both disturbed and undisturbed forest habitats

	Week numbers commencing 26.5.94–18.7.94							
Habitat	1	2	3	4	5	6	7	8
Semi-evergreen	——	——	——	——				
	- - - -	·····	- - - -	·····				
Evergreen					——	——	——	——
					- - - -	·····	- - - -	·····

about 30 minutes to walk and due to differences in terrain and vegetation, this resulted in transects being different lengths. These transects were walked between 08:30 and 10:30 each morning and between 15:30 and 17:00 each afternoon and the duration of each recorded. Each transect was divided into sections representing subdivisions of the same general habitat (e.g. canopy gap, logging trial, path or forest edge). An accurate map of each transect route was made, including landmarks, and the boundaries of each section marked. Over 4 weeks the disturbed semi-evergreen forest was walked for 1001 person-minutes, undisturbed semi-evergreen for 894 person-minutes, undisturbed evergreen forest for 720 person-minutes, and the disturbed evergreen forest for 780 person-minutes. The sampling was carried out each day for 4 weeks, unless it was raining or it had been raining up to 1 hour previously. All the butterflies seen 2.5 m either side of the transect route and up to 5 m in front were recorded (Cheverton and Thomas, 1982; Hill *et al.*, 1995). An individual was chased and caught if necessary for positive identification. If the individual could not be identified in the field, it was killed and collected for later identification. A record of date, time, locality and species name was taken. Voucher specimens were collected and are housed at the Open University, Milton Keynes, to later be deposited at the British Museum of Natural History, London. If an individual could not be caught then a description was noted and a tentative identification made (see Appendix 1). This walk-and-count transect method originates from methods used for the Butterfly Monitoring Scheme (Pollard, 1977; Hall, 1981) across Great Britain since 1976, and also in the tropics (Cheverton and Thomas, 1982; Hill *et al.*, 1995).

The similarity between habitats and sampling methods was determined using the Dice association index M = J/min. (A, B), where J is the number of species shared in the comparison and min. (A, B) is the total number of species in the smaller of the two being compared (Wolda, 1981). Whereas the Sorensen similarity index assumes similar-sized samples, the Dice association index takes into account variation in sample size, for example, the fruit trap samples being smaller than the walk-and-count samples. This is because fruit trapping is only dealing with a guild of 60 fruit-feeding butterfly species which is a small subset of the much larger pool of butterfly species found in the South-East forested habitats. The similarity of the butterfly assemblage found in the disturbed versus the undisturbed habitat in each forest type were examined against the similarity found between the disturbed habitats in the two forest types and the undisturbed habitats in the two forest types.

The basic design of the fruit trapping method comes from work carried out in Costa Rica (De Vries, 1988; De Vries, pers. comm.). In each of the four habitats, there were four locations where both a canopy (minimum of 10–15 m off the ground) and an understorey trap (1 m off the ground), were placed. The four traps in each habitat were baited, placed in the canopy and then run for five consecutive days. This sampling was repeated for another 5 days, 2 weeks later (Table 1). The traps were baited at dawn and then inspected in the early morning and late afternoon every day during the trapping period. For species which could be identified in the field, their presence in the traps was recorded and they were marked and released, otherwise they were collected. A canopy photograph was taken and a 20 × 10 m quadrat set up to calculate tree basal area at each of the fruit trap locations along the walk-and-count transect route.

Species were assigned one of two geographic range size classes for a preliminary comparison of restricted and wide ranging species within the undisturbed and disturbed forest habitats (Appendices 1 and 2).

Butterfly identification

Butterflies in the subfamilies Papilionidae, Pieridae Nymphalidae and Riodinidae were identified using D'Abrera (Parts 1–6), Barcant (1970) and De Vries (1987). The *Archaeoprepona* and *Prepona* species (Nymphalidae: Charaxinae) were identified using Papworth (1981). Members of the Satyridae euptychiine species were all placed in the *Cissia* genus, following Singer and Ehrlich (1993). Members of the Hesperiidae and Lycaenidae families were segregated according to external similarity (Appendix 1).

The analysis of species cumulative plots

The number of species encountered after the same sampling effort in each pair of habitats were compared for each forest type. In order to compare and characterize the species cumulative curves for each sampling method and habitat, a power function $S = cE^b$ was employed, where S is number of species, E is sampling effort and b and c are coefficients describing the shape and position of the curve. As the interpretation of shape (and therefore accumulation rate) was sensitive to the total number of species in a habitat, the S axis was scaled to fraction of species accumulated (S′). The function was then linearized by a log-log transformation and $\log_e S'$ regressed against $\log_e E$. This provided estimates of b (with errors), allowing statistical comparison between the disturbed and undisturbed habitats to be made, and also between the two sampling methods in the same habitat.

Measurement of tree basal areas and canopy openness

Tree basal area should be negatively correlated with canopy openness because (a) crown area is usually linearly related to the basal area of a tree (Heinsdijk, 1953; Swellengrebel, 1959) and (b) canopy openness increases with increased removal of basal area (Steege *et al.*, 1994).

Basal area was determined in 10 m × 20 m quadrats at each of 10 points along the butterfly walk-and-count transects in each forest habitat. A girth at breast height (gbh) measurement was taken for each tree > 10 cm gbh, the tree identified, and its co-ordinate recorded. To determine relative openness, photographs of the canopy from 40 cm above ground level were taken using a 35 mm lens, in the centre of each of these quadrats. From these photographs, canopy openness values were evaluated using IMAGE, a public

domain software package. This program was used to express the light area of the photograph (canopy openness) as a percentage of the total image area.

Results

Butterfly species richness and habitat similarity

In the walk-and-count transects, the two most disturbed habitats in both forest types studied had the highest species richness values and much higher numbers of individuals (Table 2). The species richness values in combined canopy and understorey fruit traps was found to be very similar between disturbed and undisturbed habitats in each forest type (Table 3). There were generally less species caught in the canopy in all habitats and considerably fewer individuals.

Moderately similar butterfly assemblages were found when comparing the walk-and-count survey data for the disturbed and undisturbed habitats in each forest type (Dice association index values of 0.54 and 0.56, Table 4). Greater similarity values were obtained when the butterfly assemblages were compared for the two disturbed habitats in the two different forest types (0.63), and likewise, for the two undisturbed forest habitats (0.65) (Table 4).

Higher association index values were found in the understorey (0.75 and 0.63) than in the canopy fruit traps (0.67 and 0.25) when the butterfly assemblages in the disturbed and undisturbed habitats in each forest type were compared (Table 4). Strong similarity in the understorey fruit trap butterfly assemblages was also seen when the butterfly species in the two disturbed habitats (0.77) and the two undisturbed habitats (0.88) were compared. In contrast, the faunas in the canopy fruit traps in the same comparisons were strongly dissimilar (0.25 and 0.43 respectively, Table 4).

Table 2. Butterfly species richness and total number of individuals found in a disturbed and undisturbed habitat in two forest types, for the walk-and-count sampling

	Semi-evergreen		Evergreen		
Habitat	Disturbed	Undisturbed	Disturbed	Undisturbed	Total
Observed number of species (S)	47	37	40	22	80
Number of individuals (N)	390	184	331	41	946

Table 3. Butterfly species richness-and number of individuals caught in fruit traps set in the canopy (C), understorey (U) and both forest strata together, in a disturbed and undisturbed habitat in two types of forest

	Semi-evergreen						Evergreen					
Habitat	Disturbed			Undisturbed			Disturbed			Undisturbed		
Fruit trap	All	U	C	All	U	C	All	U	C	All	U	C
Number of species	17	17	6	17	13	8	11	9	4	15	10	9
Number of individuals	146	133	13	102	86	16	89	66	23	48	34	14

Table 4. Dice association index values of the similarity of butterfly assemblages between disturbed (D) and undisturbed (U) forest habitats in two types of forest and between forest types in disturbed and undisturbed habitat. Comparisons are made for species encountered on walk-and-count transects and in understorey, canopy and combined (both understorey and canopy) fruit traps

	Semi-evergreen D vs U	Evergreen D vs U	D vs D	U vs U
Walk-and-count transect	0.54	0.56	0.63	0.65
Understorey fruit traps	0.75	0.63	0.77	0.88
Canopy fruit traps	0.67	0.25	0.25	0.43
Combined fruit traps	0.67	0.55	0.64	0.75

In every comparison made between the similarity of butterfly assemblages found using walk-and-count and fruit trapping techniques, the greater similarity values were found in the disturbed habitat rather than the undisturbed and in the understorey rather than the canopy (Table 5).

Species cumulative plots

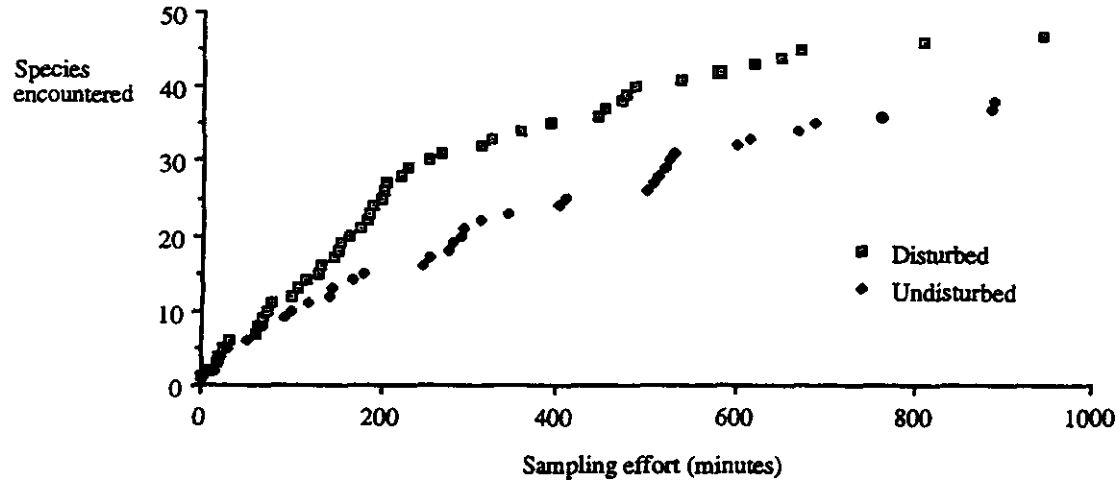
Species cumulative plots were carried out for butterfly species encountered in each habitat during four weeks of walk-and-count transects (Fig. 2). For the semi-evergreen disturbed and undisturbed habitats the species cumulative plots were curvilinear and asymptotic, implying that fewer additional species were being encountered. The undisturbed evergreen plot, however, was linear, and the latter part of the disturbed close to linear, implying that a lot more sampling effort was needed before the total number of species would be encountered.

When rates of species accumulation (slope of the log fraction of species accumulated against log sampling effort) were compared between habitats for the walk-and-count data, it was found that the habitats were ranked: undisturbed evergreen < undisturbed semi-evergreen < disturbed semi-evergreen < disturbed evergreen (Table 6). The rates of species accumulation for the two undisturbed habitats were not significantly different from one another ($F = 3.95, p > 0.05$, df = 1,55), but species accumulated significantly slower in the undisturbed evergreen habitat than both the disturbed evergreen habitat ($F = 6.47$, $p < 0.05$, df = 1,64) and the disturbed semi-evergreen habitat ($F = 4.60, p < 0.05$, df = 1,64). There was no significant difference in species accumulation rate between the undisturbed semi-evergreen and either the disturbed semi-evergreen habitat ($F = 0.027$, $p > 0.05$, df = 1,81), or the disturbed evergreen habitat ($F = 0.40, p > 0.05$, df = 1,81),

Table 5. Similarity values, using the Dice association index, of species assemblages found between walk-and-count transects and fruit trapping in the understorey, canopy and both (understorey and canopy combined)

	Semi-evergreen		Evergreen	
	Disturbed	Undisturbed	Disturbed	Undisturbed
Understorey	0.75	0.58	1.00	0.38
Canopy	0.50	0.29	0.75	0.13
Combined	0.75	0.47	0.91	0.25

a) Semi-evergreen forest



b) Evergreen forest

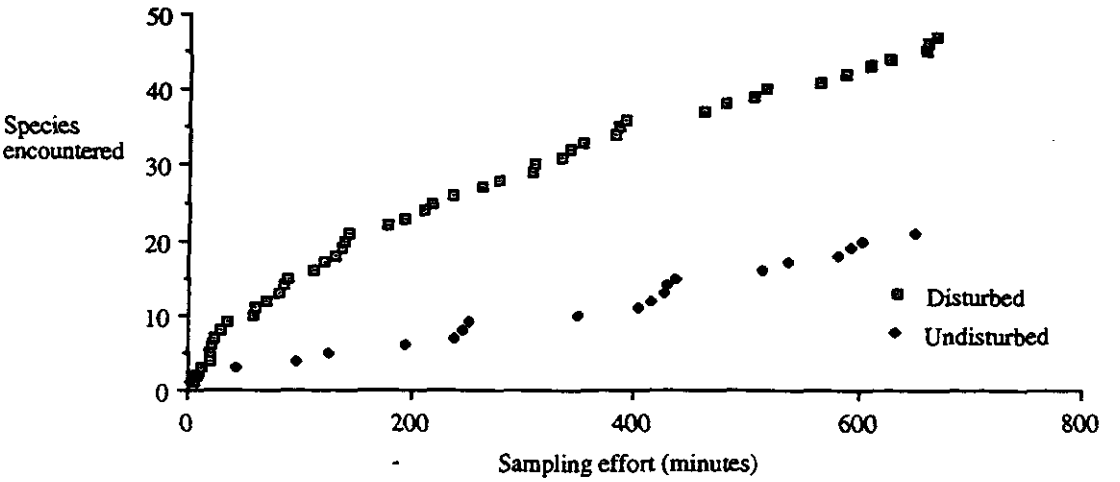


Figure 2. Species accumulations with sampling effort for walk-and-count transects in (a) semi-evergreen forest and (b) evergreen forest.

or between the disturbed semi-evergreen and the disturbed evergreen habitat ($F = 0.23$, $p > 0.05$, df = 1,90).

Species cumulative plots were also made from combining the understorey and canopy fruit trap data (Fig. 3). Here species richness values after 1728 trap hours were the same for the disturbed and undisturbed habitat in the semi-evergreen forest, both accumulating 17 species. The undisturbed habitat species cumulative curve, however, was more linear

Table 6. Summary of regression statistics for log fraction of species accumulated against log sampling effort for the two sampling methods (F = fruit trap data, W = walk-and-count data)

	Semi-evergreen				Evergreen			
	Disturbed		Undisturbed		Disturbed		Undisturbed	
	F	W	F	W	F	W	F	W
Regression coefficient	0.714	0.649	0.643	0.641	0.352	0.670	0.574	0.536
SE	0.085	0.016	0.021	0.011	0.030	0.017	0.038	0.034
r^2	0.909	0.972	0.988	0.989	0.978	0.973	0.965	0.929

than the disturbed habitat. In the evergreen forest, 1440 trap hours trapped 15 species in the undisturbed habitat and 11 in the disturbed.

The ranking of the species accumulation rates for the fruit trap data were found to be: disturbed evergreen < undisturbed evergreen < undisturbed semi-evergreen < disturbed semi-evergreen (Table 6). The rate of accumulation of fruit-feeding species in the disturbed evergreen habitat, found to be the highest with the walk-and-count data, was the lowest with the fruit trap data. In fact species accumulated at a significantly lower rate in the disturbed evergreen habitat compared to any of the other three habitats (undisturbed evergreen, $F = 37.93$, $p < 0.001$, df = 1,22; undisturbed semi-evergreen, $F = 48.92$, $p < 0.001$, df = 1,24; disturbed semi-evergreen, $F = 70.78$, $p < 0.001$, df = 1,24). The undisturbed evergreen habitat accumulated species significantly slower than the semi-evergreen disturbed habitat (as found with the walk-and-count, data, $F = 13.65$, $p < 0.001$, df = 1,28) but was not significantly different from the other undisturbed habitat in the semi-evergreen forest ($F = 3.89$, $p > 0.05$, df = 1,28).

When species accumulation rates were compared between the two butterfly sampling methods used in each habitat, there was found to be no significant difference for three of the habitats (undisturbed evergreen, $F = 0.49$, $p > 0.05$, df = 1,32; undisturbed semi-evergreen, $F = 0.0006$, $p > 0.05$, df = 1,51; disturbed semi-evergreen, $F = 1.17$, $p > 0.05$, df = 1,60), but a highly significant difference for the disturbed evergreen habitat ($F = 14.76$, $p < 0.001$, df = 1,54).

Tree basal areas and canopy openness

There was a significant difference between the mean basal areas of the 4 habitats (Table 7; one-way ANOVA, $F = 3.124$; df = 3,36; $p = 0.038$). However, there was only a significant difference between the undisturbed evergreen forest mean basal area value and that of the disturbed semi-evergreen forest, which was approximately half the former (Tukey T-Method test (Sokal and Rohlf, 1981), MSD = 26.65; $p < 0.05$). The disturbed and undisturbed semi-evergreen and disturbed evergreen forests were not significantly different in basal area. The basal area of the undisturbed evergreen forest in Trinidad was similar to that found in Jamaican primary forest (Tanner *et al.*, 1987, Table 7).

Mean canopy openness values were obtained (Table 7) which were not significantly correlated with tree basal areas for either the disturbed semi-evergreen habitat ($r = 0.549$; df = 8; $p > 0.05$), the undisturbed evergreen forest habitat ($r = 0.144$; df = 8; $p > 0.05$) or for both habitats ($r = 0.238$; df = 16; $p > 0.05$). Although mean canopy openness values for these two habitats with the greatest difference in mean basal area were fairly similar,

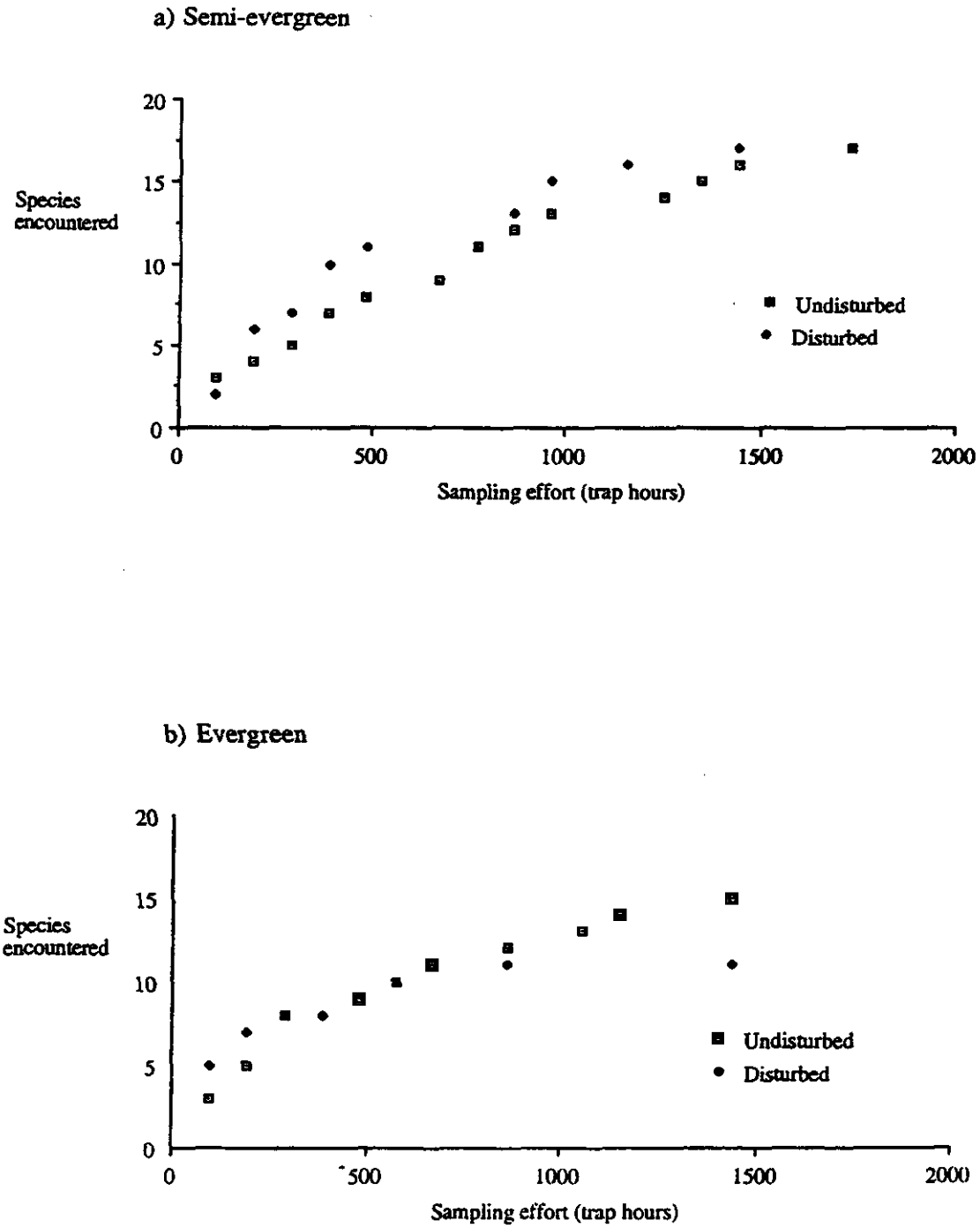


Figure 3. Species accumulations with sampling effort for fruit-trapping in the combined understorey and canopy of (a) semi-evergreen forest and (b) evergreen forest.

the variance (s^2) in canopy openness values was much greater for the disturbed semi-evergreen habitat than the undisturbed evergreen forest (disturbed semi-evergreen mean openness = 7.61; $n = 10$; $s^2 = 45.6$ and undisturbed evergreen forest mean openness = 11.0; $n = 10$; $s^2 = 1.17$).

Table 7. Comparison of tree basal areas and canopy openness values for four different forest habitats in Trinidad (T) and for a tropical lowland forest below 600 m in Jamaica (Tanner *et al.* in Swaine *et al.* (1987))

Forest habitat	Min. gbh (cm)	Basal area (m^2 ha^{-1})	SE	Mean canopy openness (%)	SE
Evergreen undisturbed forest (T)	10	62.95	0.692	11.0	1.08
Evergreen disturbed(T)	10	38.05	0.374	12.3	6.99
Semi-evergreen undisturbed(T)	10	37.0	0.383	4.94	2.66
Semi-evergreen disturbed(T)	10	33.2	0.426	7.61	6.75
Primary forest (Jamaica)	10	65.4	–	–	–

Discussion

The walk-and-count census carried out in South-East Trinidad revealed that butterfly species richness was greater in the disturbed forest habitats. Species accumulation functions (Fig. 2) clearly show this disparity in species richness in habitats, the more disturbed habitats in both forest types having 21 and 110% more species than the undisturbed habitats over the same sampling period. Workers in the Amazon forests of Brazil also reported greater butterfly species richness in more disturbed areas (Lovejoy *et al.*, 1986; Brown, 1991). In Costa Rica, a road transect, following a wide, continuous light-gap, produced 74% more butterfly species than a trail transect that traversed undisturbed forest with scattered light gaps (Sparrow, 1994). Work carried out in Malaysia found both butterfly species richness and diversity to be higher in unlogged forests than in logged forests (Hill *et al.*, 1995). Work in forest fragments in Manaus, Brazil, also showed a dramatic increase in butterfly species richness in forest habitats with increased light levels in the understorey, such as in large internal clearings and fragments which were semi-isolated (increased proportion of edge habitat), compared with inside forest (Brown, 1991). These results have parallels in temperate forest habitats where the management of forest and rides to provide a large range of shade levels, has been found to increase the number of habitats suitable to different butterfly species (Warren, 1985).

Comparison of walk-and-count species accumulation rates between habitats (the slower the accumulation rate the greater the evenness of the butterfly assemblage in that habitat) revealed that the undisturbed evergreen habitat was significantly lower than the two disturbed habitats, but not significantly different from the other undisturbed habitat (Table 6). Thus the apparent lower species richness in undisturbed forest may be due to the short sampling effort.

Comparisons of fruit trap species accumulation rates also found no significant difference between the undisturbed habitats. The highest species accumulation rate for the disturbed evergreen forest habitat from walk-and-count data, however, was found to be significantly lower than all other habitats for the fruit trap data. From the species cumulative curves (Fig. 3) it can be seen that five of the 11 species encountered through fruit trapping in the disturbed evergreen habitat were encountered in the first 96 trap-hours of trapping. The next 1344 trap-hours added only six more species to the list. Through walk-and-count sampling, new species were continually encountered over the sampling period in the disturbed evergreen habitat. By also using an alternative sampling method, fruit trapping, a completely different picture of species accumulation was unveiled. Only

through the concurrent use of these two sampling methods was this difference between butterfly assemblages within the same habitat detected. Furthermore, the importance of using measures of accumulation rate to describe a habitat's butterfly fauna, in addition to species counts, is clear, as very different interpretations of forest disturbance may result from the use of these two species measures.

These results could reflect the true composition of the butterfly assemblages or could be due to the relative effectiveness of the butterfly sampling methods used. The detectability of butterflies on walk-and-count transects was probably lower in the darker understorey of the undisturbed forest habitats than in the disturbed habitats. Whilst we might expect to detect slightly fewer individuals in the undisturbed habitat, the differences in visibility between the undisturbed and disturbed habitats were small and unlikely to have led to significant differences in species detection rates.

The species richness of insect communities in rainforest canopies has been documented in a few widely cited examples (Erwin, 1983; Stork, 1988). The species richness of the butterflies in the canopy is only known from a few examples involving fruit trapping (DeVries,1988) or direct observation (Hill, 1992). It is the general impression of DeVries that any Costa Rican forest habitat below 1900 m has a higher butterfly diversity in the canopy than in the understorey, although he admits more work is needed (DeVries, 1987). Disturbance, however, can disrupt this stratification between the canopy and understorey faunas. DeVries has stated that 'butterflies treat disturbances as if the canopy had come to the ground' (DeVries, 1987) and 'if differences in light levels are important for maintaining stratification in rainforest butterflies, we might predict that in habitats without pronounced differences in light levels (i.e., disturbed forest, in deciduous forest in the dry season, or along forest edge), stratification will not be as distinct as in closed canopy forest' (DeVries, 1988). This was highlighted in the present study when the butterfly faunas sampled by walk-and-count transects were compared to those caught in the canopy fruit traps. High dissimilarity was evident in the two undisturbed habitats sampled (mean Dice association index value of 0.21) whereas similarity was much greater in the disturbed habitats (mean association index value of 0.61). This suggests that the canopy of the disturbed forest habitats are too disturbed to maintain a distinct canopy fauna from an understorey one, but the undisturbed habitats do have a stratified butterfly assemblage.

The butterfly assemblages encountered through walk-and-count surveys in the same disturbance level (i.e. both disturbed or both undisturbed habitats in different forest types) showed greater similarity than between the disturbed and undisturbed habitat in the same forest type (Table 4). This implies that within a region of forest, butterflies are characteristic of disturbance rather than forest vegetation type. This lends further weight to the belief that butterfly faunas can be used as bioindicators of disturbance. For the fruit trapped butterflies, the understorey butterfly assemblages were more similar than the canopy butterfly assemblages between the disturbed and undisturbed habitats in the same forest type, and in different forest types within the same disturbance category (Table 4).

Fruit-trap studies are by design only sampling the relatively small guild of fruit-feeding butterflies, approximately 60 species for Trinidad (Barcant, 1970). This would suggest that the number of species encountered when fruit trapping would be less than the number encountered on walk-and-count transects, which was indeed the case. Furthermore, despite 1500 trap hours of sampling, it is likely that the plots were far from capturing the total number of species in each habitat. This was shown to be the case when the data for the 864 trap hours (four traps) of fruit trapping in the understorey of the

undisturbed semi-evergreen forest in 1994 was compared with data over 10 000 trap hours (18 traps) in 1995 at the same site (Fig. 4). Despite the difference in total number of species, of the 13 species encountered in 1994, seven were in the top 10 most abundant species for 1995. Hence the fruit trapping in this study (1994 data) and the comparisons made between habitats, is likely to be amongst the most abundant species in each habitat. This fact, combined with the use of accumulation functions (which were all based on highly significant overall fits to the data), suggest that relatively short sampling periods can provide valuable insights into the response of the core of the butterfly assemblage to disturbance.

While the importance of undisturbed habitats for certain butterfly species is clear, this work has shown that disturbed forest habitats also have a part to play, providing a rich mosaic of microhabitats varying in light and abiotic conditions, attracting secondary-growth, lightloving butterflies from the forest edge (Lovejoy *et al.*, 1986; DeVries, 1988; Brown, 1991; Sparrow, 1994; Hill *et al.*, 1995). Butterfly species with narrow geographic ranges have been thought less able to make use of human-modified environments than more widely distributed species (Thomas, 1991), and forest disturbance is therefore more likely to affect endemic species adversely. However, several more restricted range species, such as *Cissia penelope*, *Catoblepia berecynthia and Pierella hyalinus* were not found to be adversely affected by forest disturbance at this level (Appendices 1 and 2).

It therefore seems likely that any conclusions about the extent of tropical forest disturbance which can be tolerated, may be taxon specific, a point also made by Margules *et al.* (1994). Termite species richness in southern Cameroon was found to be greatest in old secondary and plantation forest, followed closely by near primary forest, the least disturbed habitat, and lowest in two severely disturbed plots (Eggleton *et al.*, 1995). This enhancement in species richness at intermediate levels of disturbance (Connell, 1978) is in contrast to the pattern observed with termite species in Sarawak (Collins, 1980) and other invertebrate groups such as moth species in Malaysia (Holloway *et al.*, 1992) and scarab beetles in Manaus, Brazil (Klein, 1989), where a decrease in species richness and species diversity was found as forest habitats became more disturbed and fragmented. This pat-

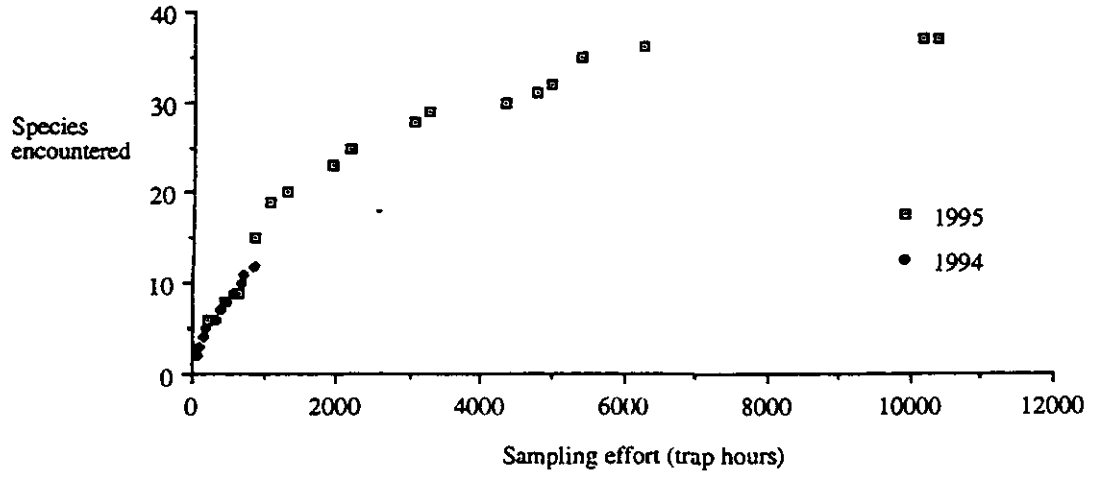


Figure 4. Species accumulation with sampling effort for fruit-trapping in the understorey of the undisturbed semi-evergreen habitat in 1994 compared with data collected in 1995.

tern is also observed with bird species, where increased levels of disturbance and increased light levels one year after selective logging in French Guiana, resulted in an overall 27–33% decrease in species richness (Thiollay, 1991). A reduction in both the number of understorey bird species and their abundance was also found by workers looking at the edge effects of forest fragmentation in Brazil (Lovejoy *et al.*, 1986) and in peninsular Malaysia (Johns, 1986). Work on the effects of eucalyptus forest fragmentation on a scorpion *Cercophonius squama* and an amphipod in South-east Australia, discovered that the abundance of scorpions did not change significantly with fragmentation, whereas amphipod abundance decreased markedly (Margules *et al.*, 1994).

In conclusion, intermediate levels of disturbance may increase species richness (Connell, 1978) but the levels will be different for different taxa and may occur very close to the natural disturbance level in primary forests. The optimal strategy for safeguarding butterfly species richness under natural forest management regimes is the maintenance of a mosaic of habitats that include areas of undisturbed primary forest and a network of forest patches, varying in management regimes and levels of disturbance.

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Appendix 1. Butterfly species abundance data from walk-and-count transects. The unnamed species listed under Riodinidae, Lycaenidae and Hesperiidae have been segregated according to external similarity. Representatives of these species have been collected. All Satyrid euptychiines are placed in the genus *Cissia* following Singer (1993). Species ranges were placed in one of two categories, either widespread category (1) Neotropical; occurring in Central and South America, or the more restricted category (2) Amazonia + Venezuela/Guianas/Columbia. Range data from Barcant (1970), DeVries (1987) and D'Abrera (1981–96)

	Semi-evergreen		Evergreen		
Butterfly species	D	U	D	U	Range
Satyrinae					
Pierella hyalinus	14	14	57	8	2
Taygetis andromeda	1				1
T. echo	1		2		2
T. penelea	13	5		1	1
T. virgilia	6				1
Cissia penelope	16	6	96	2	2
C. hermes	20	39	41	6	1
C. hesione	14	2	11		1
C. myncea	3				2
C. libye	4		4	2	1
C. terrestris			1		1
C. arnaea		6	10		1
C. junia	2	1	1	1	2
C. cephus	1	4	13	1	2
Danainae					
Lycorea (cleobaea) ceres	1			1	1
Ithomiinae					
Aeria eurimedia		2	1		1
Mechanitis (polymnia) isthmia	28	6	2		1
M. menapis	1				1
Melinea (ethra) lilis	1				1
Tithorea harmonia	127	20			1
Hypoleria ocalea	3				2
Ithomia pellucida	1				2
Heliconiinae					
Heliconius melpomene/erato	39	6	20	2	1
H. wallacei	1	2			2
H. sara	1				1
H. ricini		2			2
Eueides isabella			1		1
Nymphalinae					
Adelpha sp			1		
Colobura dirce		3	3	1	1
Catagramma astarte		1			2

Appendix 1. (*Continued*)

Butterfly species	Semi-evergreen D	Semi-evergreen U	Evergreen D	Evergreen U	Range
Pyrrhogyra tipha				1	2
Marpesia petreus				1	1
Morphinae					
Morpho peleides	5	9	5	1	1
Brassolinae					
Caligo sp	4	8	6		
Catoblepia berecynthia	1		3		2
Eryphanis automedon	3				1
Papilionidae					
Parides sesostris			1		1
Parides sp	10				
Papilio anchisiades	1				1
Pieridae					
Phoebis sp			1		
Eurema sp	1		1		
Aphrissa statira	2				1
Riodinidae					
Nymphidium spp	1	4	11	3	
Nymphidium mantus			1		2
Lymnas (*Melanis*) *iarbus*	12		1		1
Melanis (*Isapis*) *agyrtus*		1			1
Mesene phareus			3		1
Riodinid sp 1		5	2	1	
Riodinid sp 2	1		3	1	
Riodinid sp 3		1			
Lycaenidae					
Arawacus linus		7			
Lycaenid sp 1		7	12	1	
Lycaenid sp 2			3	1	
Lycaenid sp 3	1	1			
Lycaenid sp 4	4			1	
Hesperiidae					
Hesperid sp 1	1	1	3		
Hesperid sp 2	13	2	3	1	
Hesperid sp 3			1		
Hesperid sp 4			2		
Hesperid sp 5			1		
Hesperid sp 6			1		
Hesperid sp 7		1	3		
Hesperid sp 8	3	2	2		
Hesperid sp 9	17	2	5		

Appendix 1. (*Continued*)

Butterfly species	Semi-evergreen D	Semi-evergreen U	Evergreen D	Evergreen U	Range
Hesperid sp 10			6		
Hesperid sp 11	1				
Hesperid sp 12	1				
Hesperid sp 13	3				
Hesperid sp 14	1	1			
Hesperid sp 15	1				
Hesperid sp 16	3				
Hesperid sp 17	1				
Hesperid sp 18	1				
Hesperid sp 19		4		3	
Hesperid sp 20		3			
Hesperid sp 21		1			
Hesperid sp 22		1			
Hesperid sp 23		1			
Hesperid sp 24		1			
Hesperid sp 25				1	
Total	390	182	344	41	

Appendix 2. Butterfly species abundance data from fruit traps. Data from canopy (C) and understorey (U) fruit traps in four forest habitats

Butterfly species	Semi-evergreen Disturbed U	Semi-evergreen Disturbed C	Semi-evergreen Undisturbed U	Semi-evergreen Undisturbed C	Evergreen Disturbed U	Evergreen Disturbed C	Evergreen Undisturbed U	Evergreen Undisturbed C	Range
Satyrinae									
Pierella hyalinus					1				2
Taygetis penelea	8		1						1
T. virgilia	3								1
T. andromeda	3								1
Cissia myncea	3	1							2
C. penelope	51		43		16		10		2
C. hesione	6		3		2		2		1
C. renata		-					1		1
C. hermes	6		1		1				1
C. arnaea					5				1
C. cephus						1			2
C. junia	1								2
C. terrestris	2								1
Brassolinae									
Opsiphanes cassiae	19	4	1				4	1	1
O. cassina	3	2		1				1	1

Appendix 2. (*Continued*)

Butterfly species	Semi-evergreen				Evergreen				Range
	Disturbed		Undisturbed		Disturbed		Undisturbed		
	U	C	U	C	U	C	U	C	
Caligo sp	2				12				
Caligo teucer	5		5	2			2		
Caligo eurilochus	2	1	6				2	1	
Eryphanis automedon	7	1	1	1			1		1
Catoblepia berecynthia	7			1	1			1	2
Morphinae									
Morpho peleides	3		6		9	2	5		1
Nymphalinae									
Colobura dirce	2	4	16	5	19	17	6	4	1
Archaeoprepona demophon				4					2
A. amphimachus							1	3	1
A. meander						3			1
Prepona omphale			1	1				1	1
Memphis sp								1	
M. eribotes			1						2
M. morvus			1						1
Siderone marthesia				1					1
Catagramma astarte								1	2
Total	133	13	86	16	66	23	34	14	

Appendix B.1

Table of fruit-feeding species and geographic ranges for butterfly species encountered on walk-and-count transects (W), fruit-traps (F) and observed that year but not when sampling (S), in the studies for Ch. 3 (1994) and Ch.4 (1995). Numbers of new captures in parantheses. Numbers caught in fruit traps refer to understorey traps unless followed with 'c' which refers to the number caught in canopy traps.

SPECIES	YEAR OF STUDY		GEOGRAPHIC RANGE
	1994	**1995**	
Satyrinae			
Pierella hyalinus Gmelin	F(1);W(93)	F(18)	Amazonas, Guianas, Venezuela and Trinidad
Taygetis andromeda Cramer	F(3);W(1)	F(116)	Mexico to Guianas to Paraguay
T. echo Cramer	W(1)	F(21)	Venezuela, Amazonas (Ecuador, Brasil, ?Peru), Guianas
T. penelea Cramer	F(9);W(19)	F(17)	Costa Rica to Panama to Amazonas to Guianas, Paraguay, northern Argentina
T. virgilia Cramer	F(3);W(6)	F(42)	Mexico to Brasil
Cissia penelope Fabricius	F(120);W(120)	F(1349)	Amazonas to Guianas
C. hermes Fabricius	F(8);W(106)	F(151)	South U.S.A to Uruguay
C. hesione Sulzer	F(13);W(27)	F(65)	Mexico to Amazonas, Bolivia, southern Brasil, ?Paraguay
C. myncea Cramer	F(3,1c);W(3)	F(50)	Panama to Peru, Guianas, Trinidad
C. terrestris Butler	F(2);W(1)	F(6)	Amazonas to Guianas
C. themis Butler		F(8)	Not mentioned in D'Abrera
C. renata Cramer		F(11)	Mexico to southern Brasil
C. cephus Fabricius	F(1c);W(19)	F(2)	Amazonas, Guianas, Trinidad
C. junia Cramer	F(1);W(4)	F(1)	Guianas, northern Brasil, Trinidad
C. libye Linnaeus	W(10)	F(2)	Mexico to Amazonas, Guianas, south eastern Brasil
C. arnaea Fabricius	F(5);W(16)	F(16)	Nicaragua to Amazonas, south eastern Brasil
C. brixiola Godart		F(1)	Colombia to Guianas, south eastern Brasil

SPECIES	YEAR OF STUDY		GEOGRAPHIC RANGE
	1994	**1995**	
Brassolinae			
Opsiphanes cassina merianae Stichel	F(3,4c)	F(25)	Guianas, Venezuela, Trinidad
O. cassiae Linnaeus	F(23,5c)	F(13)	Guianas, Venezuela, Trinidad
Catoblepia berecynthia berecynthia Cramer	F(7,1c);W(4)	F(32)	Guianas, Venezuela, Trinidad, central Amazonas of Brasil
Caligo eurilochus Cramer	F(36,4c);W(18)	F(61)	Guianas, eastern and central Amazonas (Venezuela, Panama)
C. teucer insulanus Stichel	F(36)	F(105)	Venezuela, Trinidad
C. illeonus polyxenus Stichel	F(36)	F(14)	Venezuela, Trinidad
Eryphanis automedon automedon Cramer	F(9,2c);W(3)	F(11)	Venezuela, Trinidad, Guianas to Rio de Janeiro in Brasil
Morphinae			
Morpho peleides insularis Fruhstorfer	F(23,2c);W(20)	F(166)	Trinidad and Tobago
Ithomiinae			
Ithomia pellucida Weymer	W(1)	F(4)	Venezuela, Trinidad and Tobago, Brasil (Bahia)
Nymphalinae			
Siproeta stelenes Blanchard		S(~10)	Southern U.S.A. to Brasil, West Indies
Biblis hyperia Cramer		F(1)	Colombia to Paraguay
H. feronia Linnaeus		F(24)	South Texas to Argentina, Brasil, Trinidad
H. amphinome amphinome Linnaeus		S(~3)	?Panama, east slopes of Andes, Amazonas to Rio de la Plata Basin

SPECIES	YEAR OF STUDY		GEOGRAPHIC RANGE
	1994	**1995**	
Nymphalinae (cont.)			
H. arethusa Fruhstorfer		S(~3)	Central Mexico to north-west Colombia, northern Venezuela, Trinidad
Catagramma astarte Kaye	F(1c)	F(1)	Trinidad, ?St. Lucia (*astarte astarte* Brasil (central and southern Amazonas) to Guianas)
Pyrrhogyra tipha Linnaeus	W(1)	F(1)	Not mentioned in D'Abrera
Adelpha iphicla Linnaeus		F(8)	Central America to Paraguay, Cuba
Temenis laothoe laothoe Cramer		F(2)	(Colombia to Bolivia, Brasil) Amazonas, Guianas, ?Trinidad, ?Curacao
Colobura dirce dirce Linnaeus	F(41,30c);W(7)	F(166)	Mexico to Paraguay
Charaxinae			
Memphis morvus morvus Fabricius	F(1)	F(2)	Amazonas, Guianas
M. eribotes Fabricius	F(1)	F(8)	Eastern Amazonas to Guianas
M. ryphea ryphea Cramer		S(1)	Mexico to Venezuela, Guianas, Trinidad, Colombia to Bolivia
Zaretis itys Cramer		F(1)	Mexico to Bolivia, Brasil, Guianas
Consul fabius ochraceus Butler		F(1)	Mexico to northern Argentina
Siderone marthesia Cramer	F(1c)		Mexico to Bolivia, Brasil, Guianas
Historis odius orion Fabricius		S(~2)	Southern U.S.A. to Argentina
H. acheronta acheronta Fabricius		F(1)	Mexico to Brasil

SPECIES	YEAR OF STUDY		GEOGRAPHIC RANGE
	1994	**1995**	
Charaxinae (cont.)			
Prepona omphale omphale Hu"bner	F(1,1c)	F(2)	Central Amazonas, Guianas to Bahia in Brasil
Archaeoprepona meander meander Cramer	F(3c)		Venezuela, Amazonas, Guianas, Trinidad
A. amphimachus amphimachus Fabricius	F(1,3c)	F(3)	(Mexico to Colombia) Venezuela, Amazonas, Guianas, Trinidad
A. demophon demophon Linnaeus	F(4c)	F(20)	Amazonas to Guianas, Mato Grosso to Bolivia
A. demophoon ilmater Fruhstorfer		F(3)	Trinidad
Riodinidae			
Mesosemia sp.		F (2)	

Appendix B.2

Total number of new captures of each species encountered in fruit traps in the four 'gaps' and four 'non-gaps' in each block, over the four week study detailed in Ch.5.

Species	30 yrs B7		5 yrs B1		0 yrs B6		TOTAL	
	Gap	Non	Gap	Non	Gap	Non	Gap	Non
Pierella hyalinus	1	1	0	0	2	0	3	1
Taygetis cleopatra	4	3	0	0	2	0	6	3
T. echo	4	3	2	1	1	0	7	4
T. penelea	1	0	0	0	0	0	1	0
Cissia penelope	0	1	3	4	17	1	20	6
C. hermes	0	0	0	0	4	1	4	1
C. hesione	0	0	3	0	4	3	7	3
C. arnaea	36	17	8	9	1	3	45	29
C. myncea	1	0	1	1	1	2	3	3
C. terrestris	0	1	1	0	1	0	2	1
C. libye	0	0	0	0	1	0	1	0
C. cephus	0	1	0	0	0	0	0	1
Morpho peleides	2	3	1	0	0	1	3	4
Caligo spp.	3	4	5	6	2	2	10	12
Catoblepia berecynthia	1	1	1	3	0	1	2	5
Opsiphanes cassiae	1	2	0	2	1	1	2	5
Colobura dirce	5	10	21	13	24	14	50	37
Archaeoprepona demophon	0	0	0	1	0	0	0	1
A. amphimachus	0	0	0	1	1	0	1	1
Historis odius	0	0	0	0	2	0	2	0
Temenis laothoe	0	0	0	0	1	0	1	0
TOTAL	59	47	46	41	65	29	170	117

Appendix C.1

Mark-release-recapture data for *Cissia penelope* in study 2, for half days, illustrating a Method B table, used to calculate Jolly-Seber population estimates. Values of the following variables, defined using the terminology of Jolly (1965), are generated: m_t = Number of marked animals caught in sample t; u_t = Number of unmarked animals caught in sample t; n_t = Total number of animals caught in sample t = $m_t + u_t$; and s_t = Total number of animals released after sample t = (n_t - accidental deaths or removals)

| Time of last capture | Time of capture | | |

Appendix C.2

C. penelope open population estimates for study 2 (18 fruit traps) over 23.5 trapping days (47 half days). * Refers to population estimates derived on days when no individuals were trapped, from the average of the 4 nearest estimates either side of that half day. - No estimate can be made of this parameter from the data available.

Sample (half days)	Proportion marked (a_t)	Size of marked population (M_t)	Population estimate (N_t)	Probability of survival (f_t)	Confidence limits of N_t
0.5	0	0	-	0.637	-
1.0	0.36	17.20	43.96	0.875	26.4-74.5
1.5	0.39	27.30	60.93	0.846	35.8-99.5
2.0	0.46	37.50	75.00	0.725	29.7-165.2
2.5	0.36	32.27	80.68	0.893	33.7-160.5
3.0	0.36	36.86	98.29	0.817	59.4-133.5
3.5	0.90	50.55	55.61	1.185	29.8-71.6
4.0	0.55	61.08	106.88	0.821	51.5-167.2
4.5	0.44	57.50	126.50	0.864	68.7-174.0
5.0	0.46	65.23	137.71	0.951	78.4-177.1
5.5	0.47	81.03	168.55	0.842	99.9-209.7
6.0	0.74	90.92	121.23	0.984	60.8-169.9
6.5	0.43	94.43	213.49	0.800	117.9-279.8
7.0	0.61	98.80	158.08	0.808	77.9-225.5
7.5	0.51	87.14	165.99	1.480	95.3-202.0
8.0	0.65	156.60	234.90	0.602	95.8-432.1
8.5	0.33	99.09	280.76	1.140	131.6-420.5
9.0	0.46	138.00	290.53	0.772	141.4-417.1
9.5	0.86	122.80	140.34	1.204	48.0-318.9
10.0	0.38	149.10	386.56	0.765	201.6-520.9
10.5	1.00	147.00	147.00	0.792	53.4-315.9
11.0	0.69	116.40	164.90	1.549	71.6-273.2
11.5	0.22	188.09	799.39	0.527	344.3-1317
12.0	0.39	126.54	320.30	0.649	184.2-395.6
12.5	0.74	114.00	152.00	1.156	77.1-201.5
13.0	0.45	137.61	297.41	0.790	167.1-370.4
13.5	0.56	137.07	237.58	0.979	110.8-353.1
14.0	0.46	145.00	309.08	0.632	179.4-379.5
14.5	0.32	118.81	363.03	0.888	224.6-416.6
15.0	0.55	171.16	306.29	0.839	179.2-354.6
15.5	0.61	168.72	276.31	0.593	182.9-315.9
16.0	0.70	126.06	178.34	1.429	110.5-208.7
16.5	0.63	204.43	323.68	0.293	153.9-555.6
17.0	0.37	68.09	177.78	0.754	93.8-260.0
17.5	0.61	73.18	115.87	0.969	52.8-191.5
18.0	0.51	77.70	148.15	0.671	77.9-219.9
18.5	0.67	64.88	93.71	1.272	39.1-173.2
19.0	0.46	87.60	185.71	0.447	92.2-316.9
19.5	0.44	51.63	113.08	0.953	62.8-187.2
20.0	0.62	73.00	113.57	0.664	30.0-473.0
20.5	0.43	51.14	111.58	0.521	41.3-303.6
21.0	0.64	33.40	50.10	0.840	18.0-151.6
21.5	0.34	31.43	85.71	0.430	36.0-260.0
22.0	0.70	21.67	29.79	0	10.5-186.4
22.5	0.33	-	-	-	-